THE FORAGING ACTIVITY AND PROVISIONING STRATEGIES OF ANTARCTIC FUR SEALS IN RELATION TO CHANGES IN OCEANOGRAPHIC CONDITIONS AT THE KERGUELEN ARCHIPELAGO

by

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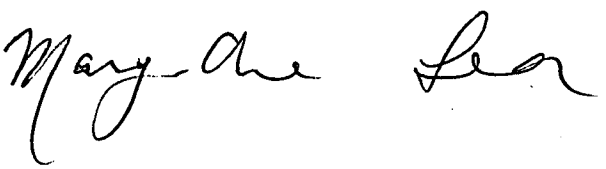

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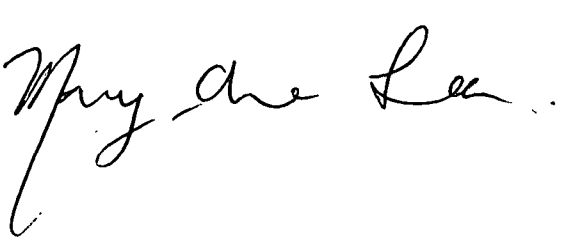

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'La plongeuse de la nuit'

In memory of

Pru Mary Thalmann

ABSTRACT

The study examined how the foraging activity, foraging efficiency and the pup provisioning of a top marine predator, the Antarctic fur seal (*Arctocephalus gazella*), were affected by inter-annual variability in oceanographic conditions and prey availability in the Antarctic Polar Frontal Zone (APFZ), in February 1998, 1999 and 2000. It formed part of a larger multidisciplinary study examining predator-prey relationships in relation to oceanographic features between Antarctic fur seals, king penguins (*Aptenodytes patagonicus*) and their mesopelagic, fish prey, myctophids. The Kerguelen Archipelago (49°07'S, 70°45'E), which is located in a region of the southern Indian Ocean characterised by considerable hydrographic complexity, was chosen as the study site.

Seals were fitted with time-depth recorders and/or satellite transmitters to study their diving behaviour and at-sea distribution. Intra-population variability in diving behaviour was studied for female fur seals from two study sites at Cap Noir and Îles Nuageuses during the three years. Dietary composition was determined and compared over the three years by (1) faecal analysis and (2) fatty acid signature analysis of milk samples, to identify both short and longer-term dietary preferences. Nocturnal transect surveys were conducted by a dedicated research vessel to estimate fish availability in the foraging zones of seals, as determined from satellite tracking of seals. The fatty acid profiles and calorific content of fish prey captured during transect surveys conducted in the fur seal foraging zones were also determined. The spatial distribution of the diving effort of the fur seals was analysed in relation to oceanographic variables (sea surface temperature, chlorophyll-a concentration, and bathymetry) using spatial analysis techniques for a range of spatial scales. The foraging parameters of female seals were subsequently related to the growth performance of their pups on a per trip basis and throughout lactation.

Inter-annual differences in foraging behaviour were identified for all parameters examined. The diving activity of seals varied inter-annually and considerably between individuals within a season. The diving behaviour of seals during one foraging trip (n=117) was categorised by cluster analysis to one of four behavioural dive groups: (1) deep divers; (2) shallow active divers; (3) shallow-divers and (4) daytime divers. The proportion of seals displaying the deep diving behaviour declined from 82% in 1998 to around 50% in 1999 and 2000, indcating changes in prey availability and accessibility. Seals at Îles Kerguelen dived consistently to greater mean depths than seals than previously recorded for this species. Energy-rich mesopelagic myctophid fish formed the majority of estimated dietary biomass consumed by seals in all years, with *Gymnoscopelus piabilis*, *G. nicholsi* and *Electrona subaspera* always comprising the three main species. However, in 1998 fur seals also preyed

heavily on icefish (*Champsocephalus gunnari*) and other fish families. Simultaneous ship-based transect surveys in the foraging areas of seals confirmed that 1998 was a year of low prey availability in the foraging areas of seals in comparison to 1999. Species caught during the surveys correlated only weakly to those species identified in seal scats, indicating a high degree of prey selectivity by seals was occurring. Fatty acid analyses of fur seal milk samples confirmed the finding of the inter-annual differences observed in dietary intake for 1999 and 2000. Levels of fat within milk samples were also significantly higher in 2000 (~53%), the year of highest apparent prey availability and female body condition, than 1999 (~43%).

Seals foraged relatively close to the colony, on the edge of the continental shelf, in 1998, with foraging zones becoming more dispersed in 1999 and 2000 as females increased their median foraging range over the three years from 111km to 215km. This behaviour coincided with a lower average chlorophyll-a concentration (mg m^{-3}) over the foraging zone of fur seals in 1998, than in the two following seasons. Anomalous warm sea surface temperatures (SST) were present within the same region in 1998, and were cooler in 1999 and 2000, indicating a migration further north of Polar Frontal waters during the study. There is also evidence to suggest that the warm SST anomaly recorded in the Kerguelen region in 1997/98 coincided with one of the largest ENSO events recorded in the central Pacific Ocean in this year.

A preferred foraging area to the northeast of the archipelago was identified, although in years of higher marine productivity foraging strategies were more diverse. In 2000, the at-sea distribution and diving behaviour of the fur seals on a fine scale reflected specific combinations of environmental variables. Seals foraging to the southeast in cool SST over the continental slope dived to shallow depths whilst those foraging to the NE of the island in warmer SST over deeper water spent greater amounts of time diving to deeper depths. The foraging efficiency of mothers (daily allocation of energy to the pup) was similar between seals foraging in the different ecoregions, in this year of high prey availability.

Despite changes in the diving behaviour and dietary intake of the fur seal females, it appears that the seals were unable to fully compensate for the changes in prey availability and prey composition in this way, as rates of pup growth was much reduced in 1998 compared to 1999 and 2000. Both maternal and pup body composition were significantly poorer in 1998 than in other years, as were rates of foraging efficiency measured as the daily mass gain of pups over a foraging cycle (combined duration of a foraging trip and subsequent shore bout). Sex-based differences in mean mass and body length prior to weaning (March) were evident

for pups, however mean growth rates during the second half of lactation in all years were similar between sexes.

The study highlights the flexible foraging strategies displayed by at top marine predator in response to changing oceanographic conditions and the importance of energy-rich myctophids in the diet of seals foraging in the Antarctic Polar Frontal Zone. Female seals adjusted their foraging behaviour, including the location of foraging zones, their diving activity and diet, and foraging efficiency, concurrently with annual changes in SST and prey availability. Parameters such as foraging efficiency over a foraging cycle and variability in mean provisioning rates (trip duration), were identified as proxies of prey availability within the foraging range of seals in 1998, 1999 and 2000, emphasising the effectiveness of using Antarctic fur seal foraging behaviour as an indicator of both food and oceanographic variability.

PUBLICATIONS

The following peer-reviewed publications have been either wholly or partially derived from work associated with this thesis:

Lea M-A, Hindell M, Guinet C, Goldsworthy SD (2002a). Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. Polar Biology 25: 269-279.

Lea M-A, Bonadonna F, Hindell M, Goldsworthy SD, Guinet C (2002b). Drinking behaviour and water turnover rates of Antarctic fur seal pups: implications for the estimation of milk intake by isotopic dilution. Comparative Biochemistry and Physiology A 132: 321-331.

Lea, M-A., Nichols, P. and G. Wilson (2002c) Fatty acid composition of lipid-rich myctophids and mackerel icefish – Southern Ocean food-web implications *Polar Biology*. 25: 843-854.

Lea, M.-A., Cherel, Y., Guinet, C. and Nichols, P. (In Press) Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown by faecal and fatty acid analyses *Marine Ecology Progress Series*

Bonadonna F, Lea M-A, Guinet C (2000). Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite tracking and time-depth recorders. Polar Biology 23: 149-159.

Bonadonna F, Lea M-A, Dehorter O, Guinet C (2001). Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal (*Arctocephalus gazella*). Marine Ecology Progress Series 223: 287-297.

Guinet C, Lea M-A, Goldsworthy SD (2000). Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands. Canadian Journal of Zoology 78: 476-483.

Guinet C, Dubroca L, Lea M-A, Goldsworthy SD, Cherel Y, Duhamel G, Bonadonna F, Donnay JP (2001). Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale dependant approach using geographic information systems. Marine Ecology Progress Series 219: 251-264.

The above papers have contributed significantly to the interpretation of data presented in this thesis and have been referred to throughout the text. Permission has been granted by Springer-Verlag to reproduce Lea *et al.* 2002a as Chapter 2.

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Being involved in this project has been an adventure, a cultural experience, and always a privilege. When it all began I hadn't even heard of this impressive and beautiful group of windy French Islands where I spent a year living in a remote field hut. Over the years I've been lucky enough to see Antarctic fur seals at just about all of their breeding sites, and after studying them at Kerguelen, have nothing but respect for the way in which they deal with the challenges of life in the variable Southern Ocean, and their accommodating attitude towards biologists.

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In Hobart, Megan Tierney instructed me in the art of blowing up dried, fatty fish and was a great teacher – thanks Megs. Barry Rumbold persevered with the freighting of equipment to Kerguelen, which sometimes proved problematic. Rob Harcourt, John Arnould and Corey Bradshaw provided helpful statistical and editorial advice. Thanks to Snakelet, Clive, Louee, Rhonda and Lou for the angst ridding Monday tennis matches, and to Kirsten, Karen, Bianca, Sue, and Louee for their friendship and support (particularly in the final stages!). There are many other friends who have kept me smiling over the years and stayed in touch when I was far away: Margie, Jaya, Murph, Carina, Eric, Lou, Luke, Sophie, Mike and Tara – thanks.

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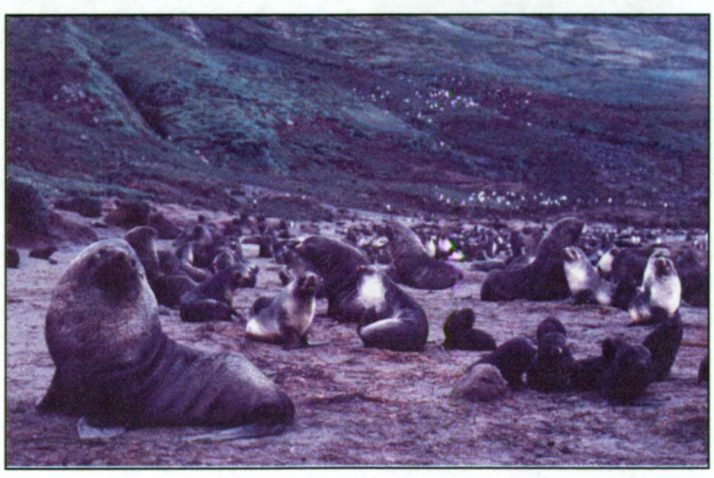
Chapter 1

General introduction



1.1 Background

Understanding how marine predators respond to fluctuations in oceanographic conditions and marine productivity are questions central to the management of both predator populations and their prey stocks. In the Southern Ocean (40-60°S) such relationships remain unexamined for many species, primarily because of the difficulty in accessing many predator populations. Until recently such logistic constraints were also coupled with a limited knowledge of environmental conditions at sea. Global datasets at various spatial and temporal resolutions are now available for many parameters such as sea surface temperature, chlorophyll-a concentration and sea surface height. Consequently, it is possible to reconstruct aspects of the marine environment concurrent to the movements and diving activity of foraging animals at sea, through the use of satellite transmitters and time-depth recorders.

Over the last two decades, studies of marine predators have focussed on two main areas of research: (1) relating annual to longer-term variation in the demographic performances of top predators to changes in environmental conditions (Croxall 1992; Barbraud *et al.* 2000; Reid 2002); and (2) relating the at-sea distribution and behaviour of predators to oceanographic conditions, which may vary considerably in marine ecosystems (Hindell *et al.* 1991; Hull *et al.* 1997; Charrassin and Bost 2002; Koudil *et al.* 2000). The Southern Ocean, in particular has received much attention with respect to these two areas of research. Many studies have shown that breeding performances of many species of seals, both in the sub-Antarctic and on the Antarctic continent, could be related to the occurrence of an El Niño Southern Oscillation (ENSO) event (Croxall 1992; Chastel *et al.* 1993; Lunn *et al.* 1993b; Guinet *et al.* 1994; 1998b). Only a few studies however, have shown that variability in breeding performances could be related to oceanographic anomalies which in turn are related to movements of the Antarctic Circumpolar Wave (White and Peterson 1996), which appear to be connected with the ENSO in the central western Pacific Ocean (Inchausti *et al.* In Press; Guinet *et al.* 1998b).

Top predators in marine systems often specialise on particular classes of prey (Croxall *et al.* 1999), and in the Southern Ocean, where the diversity of marine species is relatively low in comparison to temperate and tropical oceans (Knox 1994), the Antarctic krill (*Euphausia superba*) is a central component to the Antarctic food web. A large diversity of land-based predators depend on aggregations of krill (Veit *et al.* 1993) including species of seals (Reid and Arnould 1996); penguins (Hunt *et al.* 1992; Kirkwood and Robertson, 1997; Ainley *et al.*, 1998) and other seabirds (Croxall *et al.* 1997; Reid *et al.*, 1997). Fluctuations in the abundance and distribution of krill occur seasonally and between years (Sahrhage 1988;

Siegel 1988), and have been linked to changes in sea-ice extent, sea surface temperatures and the occurrence of climatic anomalies such as the ENSO (Priddle *et al.*, 1988; Pauly *et al.*, 2000; Loeb *et al.*, 1997). Inter-annual variability in krill availability and demography and has been shown to affect the foraging behaviour and reproductive performance of several krill predators at South Georgia (Boyd *et al.* 1995; Croxall *et al.* 1999; Reid and Croxall 2001). Thus several species of marine predators such as the Antarctic fur seal (*Arctocephalus gazella*) and the macaroni penguin (*Eudyptes chrysolophus*), for which long-term data-sets on reproductive parameters exist, have been used as indicators of prey availability and population dynamics (Reid *et al.* 1999).

The distribution of Antarctic krill, however, is limited in its distribution north by the southern boundary of the Antarctic Circumpolar Current (ACC; Orsi *et al.* 1995), a region of ecological importance (Tynan 1998). Predator species breeding on many sub-Antarctic islands, therefore must depend on other prey species. Seals (Pinnipedia) breeding on sub-Antarctic islands exhibit two different and very distinct life histories. Phocids, such as the southern elephant seal (*Mirounga leonina*), have separated the breeding and foraging phases of their life cycle both temporally and spatially (Bonner 1984). Female seals will travel thousands of kilometres from breeding sites to Antarctic waters (Jonker and Bester 1994) to feed on fish and cephalopods for the majority of the year (Slip 1995), before returning to give birth and suckle their single offspring. The large body stores gained while foraging enable females to produce milk with an extremely high lipid content (up to 60%; Hindell *et al.*1994) permitting the rapid growth of offspring during a 23 day lactation period (Fedak *et al.* 1994). Otariids such as the Antarctic fur seal, on the other hand, rear their single pup during a longer period of approximately four months (Doidge *et al.* 1986; Robinson 2002), as they must combine periods ashore suckling their pups with foraging trips to sea (attendance behaviour), due to their smaller body size and reduced energy stores. Growth rates of offspring are therefore, the integrated result of attendance behaviour, diving behaviour and milk composition of the mother (Gentry *et al.* 1986). Consequently abundant and reliable prey resources during the suckling period are influential in determining the size and body composition (fat stores) of offspring at nutritional independence. Studies of otariids across all latitudes (60°N to 60°S) have shown that several aspects of otariid maternal care, including attendance behaviour, are affected by environmental variability and ENSOs in particular (Gentry and Kooyman 1986; Trillmich and Dellinger 1991). The occurrence of such events may result in complete breeding failures in some species, such as Galapagos (*A. galapagoensis*) fur seals (Trillmich and Dellinger 1991). Such high rates of pup mortality result from starvation while pups wait for mothers to return from extended foraging trips.

In the Indian sector of the Southern Ocean, Antarctic fur seals (AFS) breed on islands, such as the Kerguelen Archipelago, within close proximity of the Antarctic Polar Frontal Zone (PFZ). Here, krill are absent and AFS, and king (*Aptenodytes patagonicus*) and macaroni penguins feed primarily on the Myctophid family of nocturnally surface migrating mesopelagic fish, which are rich in energy and highly abundant in this zone (Cherel *et al.* 1997; Klages and Bester 1998; Duhamel *et al.* 2000; Bost *et al.* 2002). Marine predators from the Kerguelen Archipelago alone were estimated to consume 460 000 tonnes of myctophids annually in 1985, with one million tonnes of estimated consumption for the same species at Îles Crozet (Guinet *et al.* 1996). Movements of the PF by 1-2° north or south occur inter-annually in this sector of the Southern Ocean (Moore *et al.* 1999a), potentially affecting both the abundance and species composition of prey available within the foraging range of Antarctic fur seals. One of the main objectives of a three-year multidisciplinary study examining the myctophid predator-prey ecosystem at Îles Kerguelen (AFS; this study, and king penguins), was to determine whether the foraging behaviour and consequent energy acquisition of marine predators was responsive to changes in oceanographic conditions and subsequent prey availability in terms of at-sea distribution and foraging efficiency. Iles Kerguelen was chosen not only for its close proximity to the PFZ, but also because of the logistic support available for conducting simultaneous surveys of prey availability, i.e. a dedicated research vessel.

The Antarctic fur seal is particularly tractable model for examining the relationship between oceanographic variability, associated changes in prey abundance and their impacts on predator foraging behaviour and reproductive performance. As central place foragers (Orians and Pearson 1979), female Antarctic fur seals are limited in their foraging range during the four-month lactation period. Because pups fast while mothers are foraging at sea, changes in the quality, distribution and abundance of prey resources could influence the maternal provisioning strategies and consequently pup growth rates and body mass prior to nutritional independence.

1.2 Objectives of the study

The main objective of the study was to determine how a top marine predator, the Antarctic fur seal, responds to inter-annual variability in a marine ecosystem (prey availability and oceanographic conditions), in terms of its at-sea distribution, foraging behaviour and efficiency, and how these parameters are related to breeding performance.

The following questions were addressed in order to examine the linkages between the foraging behaviour of mothers, variability in the marine environment and the subsequent allocation of resources to the pup over three years. Each objective essentially represents one chapter of the thesis.

- What is the at-sea distribution of female Antarctic fur seals breeding at Îles Kerguelen and can it be related to oceanographic and physical aspects of the marine environment?
- What types of diving activity are exhibited by seals, and do they vary in response to changes in the oceanic environment?
- What are the dietary preferences of seals and are they variable between years and/or in response to changes in prey availability?
- Does the spatial scale at which aspects of foraging behaviour and environmental variables are compared affect the relationship?
- How does the maternal foraging behaviour affect the growth rates, body size and body condition of pups, and does this change between years?

1.3 Study species – Antarctic fur seal (*Arctocephalus gazella*)

1.3.1 Distribution and abundance

Antarctic fur seals, *Arctocephalus gazella*, were heavily exploited by sealing throughout their range in the early 19th Century (Croxall 1992). Sought after for their valuable fur, Antarctic fur seals were exterminated at virtually all breeding sites, including South Georgia, Macquarie Island, Heard Island, Îles Kerguelen and Marion Island (Bonner and Laws 1964). Numbers remained low at South Georgia, where 95% of the species now resides (Doidge *et al.* 1986), until recovery began in around 1940 (Croxall 1992). Since then other populations throughout the Southern Ocean (Fig 1.1) have also increased at Îles Kerguelen (~10 000; Guinet *et al.* 1996), Macquarie Island (Goldsworthy, Personal Communication), Heard Island (Shaughnessy *et al.* 1988). The current population estimate for the species is approximately 1.8 million individuals (SMRU). Two genetically differentiated regions within Antarctic fur seals have recently been identified, with one region represent by populations at South Georgia, the South Shetland Islands, Bouvetoya and Marion Island, while populations at the Kerguelen Archipelago and Macquarie Island represent the other (Wynen *et al.* 2000). The most plausible explanation for such genetic variation between populations is the existence of post-sealing remnant populations of fur seals, one of which almost certainly was based on the Kerguelen Archipelago (Wynen *et al.* 2000).

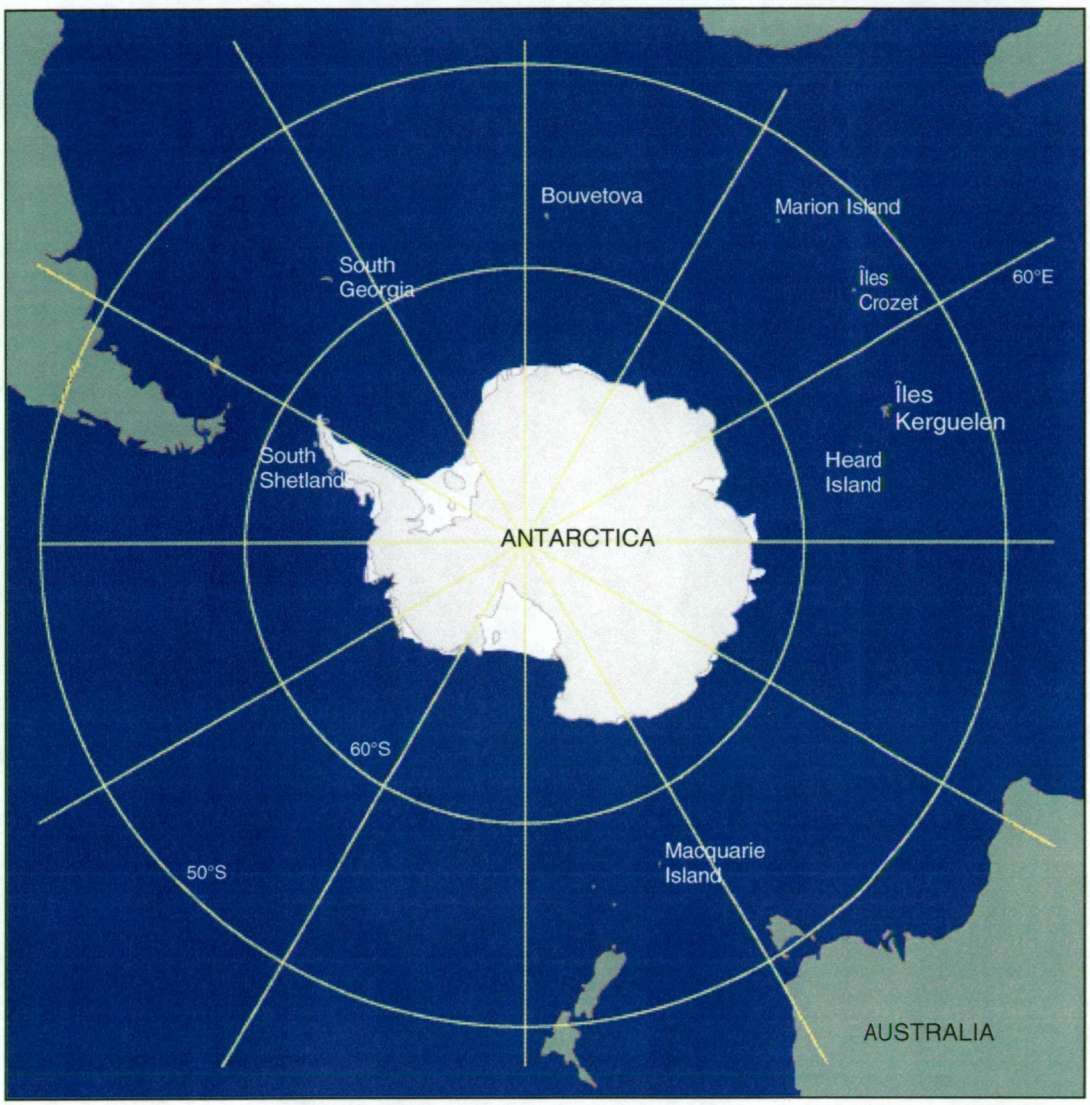


Figure 1.1 Antarctic fur seal breeding sites.

1.3.2. Breeding biology

Male seals congregate at breeding colonies from late October to early November, to establish territories. Females arrive from mid-November to late December, enter a territory and give birth to a single pup shortly thereafter. Mating occurs around six days post-partum (Doidge *et al.* 1986) after which time the female departs on the first of many trips to sea during the rearing of the pup. The lactation period is approximately 4 months, spanning the austral summer, and pups are usually weaned by late March to mid-April (Doidge *et al.* 1986; Robinson 2002). Early in the breeding season pups remain in territories while their mothers are foraging at sea. As the pups become older and more mobile, females move away from the breeding beaches into the surrounding vegetation. Pups often endure increasingly longer fasting periods, as they develop in size and the length of maternal foraging trips increases to meet their higher energy demands and/or as a response to an increased difficulty in finding food (Doidge *et al.* 1986; McCafferty *et al.* 1998; Robinson 2002).

1.3.3. Foraging ecology

Dietary preferences and aspects of foraging behaviour vary markedly between populations of *A. gazella*. At South Georgia and the Antarctic Peninsula where the majority of the species live and breed, the diet is composed primarily of krill (*Euphausia superba*), some mesopelagic fish (myctophids), notothenid fish such as icefish (*Champsocephlaus gunnari*) and occasional squid (Reid 1995; North 1996; Reid and Arnould 1996). Krill migrates to surface waters at night and dives of seals in this region are generally correspondingly shallow at 10-15 metres (Croxall *et al.* 1985a; Boyd and Croxall 1992; McCafferty *et al.* 1998; Goebel *et al.* 2000). At South Georgia lactating seals generally travel north-west towards the Antarctic Polar Front (PF) in search of prey (Boyd *et al.* 1998) spending most of their time in oceanic waters (Boyd *et al.* 2001). Inter-annual variability in foraging behaviour of seals has been observed in response to changes in prey availability and physical factors (Boyd *et al.* 1994; McCafferty *et al.* 1998a; Boyd 1999). The foraging ecology of seals at sites where fish and squid comprise the major dietary components, such as at Heard and Macquarie Islands, is more variable. At Macquarie Island, overnight foraging trips have been recorded and diving activity is also generally shallow at 12 m (Goldsworthy *et al.* 1997; Goldsworthy 1999; Robinson 2002), while at Heard Island, seals forage further afield (>200 km), regularly diving to mean depths of 10-47 m in search of prey (Green 1997). At Îles Kerguelen, where female *A. gazella* also prey primarily on myctophids (Cherel *et al.* 1997), the foraging ecology of the seals has not previously been studied.

1.4 Study site and population size

The Kerguelen Archipelago is situated in the southern Indian Ocean at 49°20' South, 70°20' East (see Fig. 1.2) and is comprised of approximately 300 islands with a combined coastline greater than 3000km. One of the most isolated land masses on Earth, it is located more than 3000km from both Africa and Australia, and approximately 2200 km north of Antarctica. The islands are the breeding site of numerous species of seabirds, penguins and marine mammals, including Antarctic fur seals and southern elephant seals (Jouventin and Stonehouse 1985; Jouventin and Weimerskirch 1990; Guinet *et al.* 1996). Historically Antarctic fur seals bred at Îles Kerguelen in large numbers until their virtual extinction by sealers in the early to mid 19th century (Budd and Downes 1969). Sporadic sightings were recorded from 1940s to 1960s and in 1984 two pups were sighted on the Courbet Peninsula to the northeast of the main island (Bester and Roux 1986).

The study colony was located at Cap Noir on the north-east coast of the Courbet Peninsula (Fig. 1.2). Today, the colony at Cap Noir extends along the coast over a distance of approximately one kilometre. Seals breed on pebbly beaches with mothers and pups moving onto the *Cotula* sp. covered slopes and plateau as the season progresses.

Counts of all visible pups at the Cap Noir colony (tagged and untagged) were made on 25 and 26 February in 1998 and in late January in 1999 and 2000 (see Table 1.1). In February 1998 pup production was estimated at 451±21 pups. The number of tagged pups sighted as a proportion of those known to be tagged was used a correction for counts of untagged pups. In January 1999 and 2000 estimates in both years ranged from approximately 725-750 pups excluding dead pups (Table 1.1). Another colony, which is similar in size, is located at Cap Rohan 4 km to the west of Cap Noir. Such a high rate of population increase since 1984 suggests that the immigration of seals from other sites, such as Îles Nuageuses to the north-west of the archipelago (Fig. 1.2), are contributing to population growth on the Courbet Peninsula (Jouventin and Weimerskirch 1990).

Table 1.1: Annual pup counts, Cap Noir colony, in 1999 and 2000

	Pups counted		Actual no.	Estimated pup
Date	Tagged	Untagged	tagged pups	production
22 Jan 1999	130	545	140	724
29 Jan 2000	137	512	158	748

1.5 Oceanographic features

The Kerguelen region, is an area of considerable hydrographic complexity (Fig. 1.3). The Antarctic Polar Front (PF), defined as the northern terminus of the 2.5°C isotherm in the

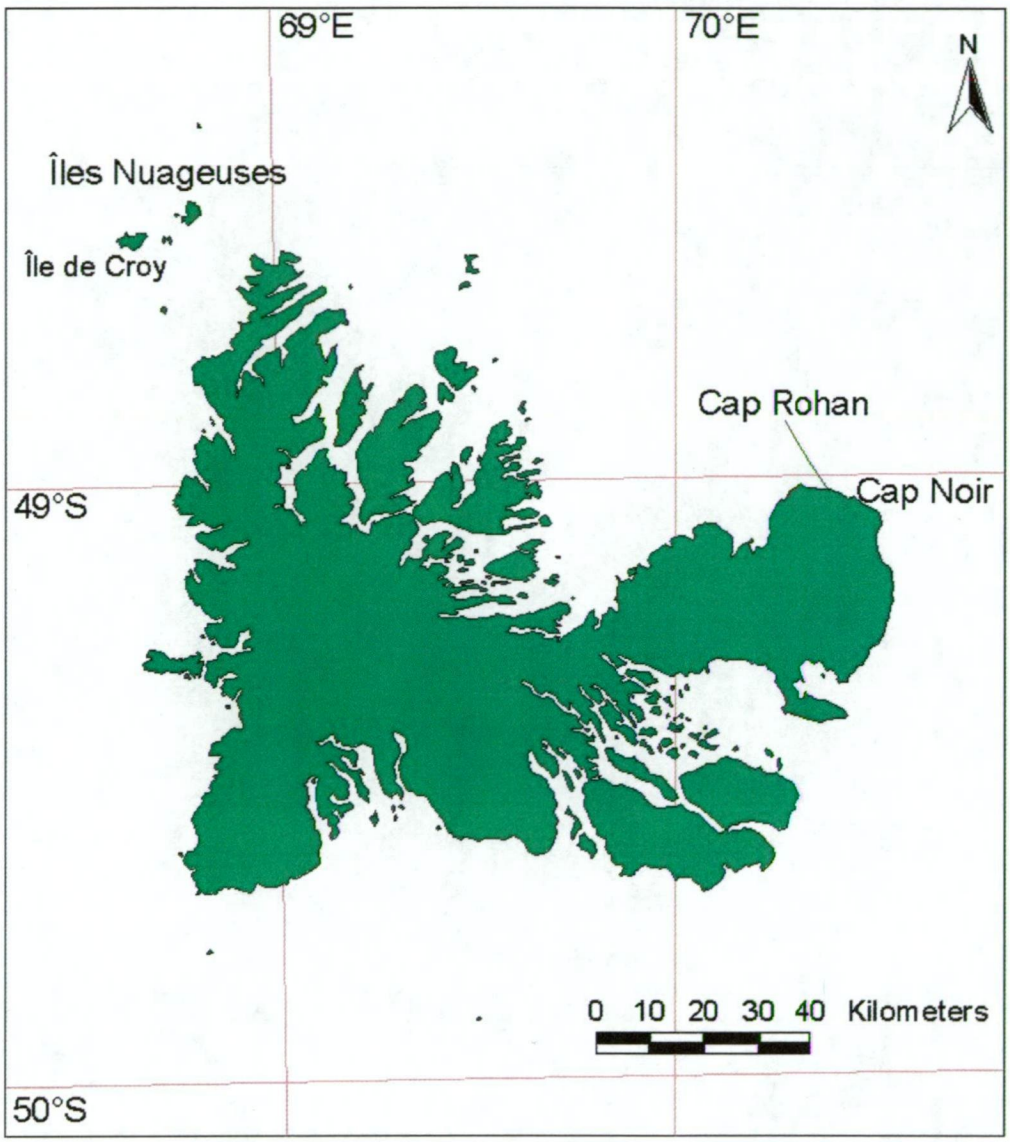


Figure 1.2 Seal colonies at the Kerguelen Archipelago, southern Indian Ocean.

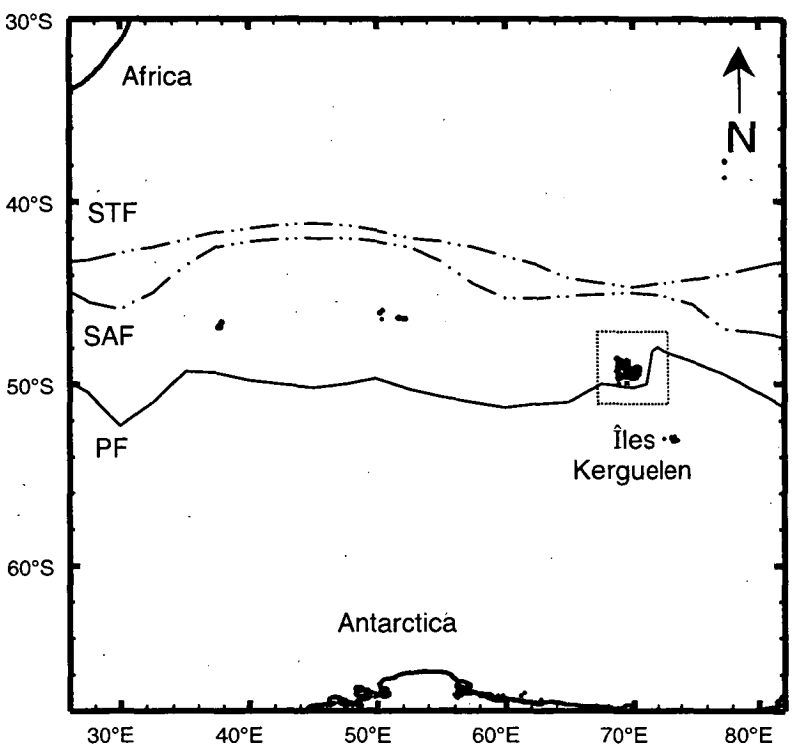


Figure 1.3 Oceanographic fronts of Southern Ocean (STF=sub-tropical front; SAF=sub-Antarctic front; PF= Polar Front) in proximity to Îles Kerguelen.

100-300m layer of the water column (Belkin and Gordon 1996), generally passes south of the Kerguelen Archipelago (Park *et al.* 1991; Sparrow and Heywood 1996) but occasionally moves north of the islands (Moore *et al.* 1999a). Bottom topography of the Kerguelen Plateau exerts strong topographic control in this region (Gambéroni *et al.* 1982; Sparrow and Heywood 1996) forcing branches of the Antarctic Circumpolar Current (ACC, Orsi *et al.* 1995) to within 2-3° of latitude to the north of the Archipelago (Park *et al.* 1991). The ACC comprises three fronts at this location (47-49°S, 65-75°E); (1) the Sub-tropical Front (STF), the (2) Sub-Antarctic Front (SAF) and (3) the PF. The STF to the north and the PF to the south bound the Polar Frontal Zone (PFZ, (Klyausov 1990; Belkin and Gordon 1996), which encompasses the Kerguelen Archipelago. The PFZ to the east and downstream of the archipelago is an area of elevated nutrients (Prego *et al.* 1999; Bucciarelli *et al.* 2001), high primary productivity (Moore *et al.* 1999b; Moore and Abbott 2000; Blain *et al.* 2001), and abundant zooplankton (Pakhomov 1997) and fish (Duhamel *et al.* 2000).

1.6 Organisation of the thesis

The foraging ecology of female Antarctic fur seals at Îles Kerguelen has been examined through the identification of annual foraging zones, inter-annual variability in diving activity, diet and milk lipid composition and through analysis of fine scale relationships between diving activity, at-sea distribution and environmental parameters. Inter-annual changes in these parameters are interpreted with respect to the climatic and oceanographic conditions surrounding the islands in 1998-2000 and the consequent impact on the breeding performance (the transfer of energy to pups) of seals in these years.

The thesis consists of six chapters: a general introductory chapter and five data chapters, the fifth of which discusses and synthesises all aspects of the study. General background for the study, objectives of the study and species and site descriptions are detailed in Chapter 1. In Chapter 2, intra-population variability in diving activity of Antarctic fur seals from two sites at the Kerguelen archipelago is examined. Chapters 3 and 4 describe the inter-annual dietary preferences of the fur seals and compositional aspects of their prey. Chapter 3 provides a detailed description of the fatty acid composition and calorific value of prey species from the Kerguelen region, while in Chapter 4 the diet composition of Antarctic fur seals, as assessed by conventional scat analysis and fatty acid signature analysis, is compared between years. Aspects of diving behaviour examined in Chapter 2 are related to fine-scale variation in oceanographic parameters within the foraging range of seals on a nightly basis in Chapter 5. In Chapter 6 all aspects of foraging ecology and maternal provisioning strategies are compared inter-annually with environmental variables and are related to the allocation of resources to the pup, as measured through growth rates and body composition in each of the

three years. Findings are also summarised and placed in the context of related ecological studies.

With the exception of the General Introduction (Chapter 1) all chapters are self-contained, are sequentially related in terms of content and have been written up as scientific papers. Consequently there is a small degree of repetition between chapters. The abstracts and reference lists for each paper have been removed and combined in the thesis abstract and reference list. As the project involved the collaboration of scientists from four laboratories in France and Australia, many of the papers have been co-authored by researchers who contributed their time in the field, their laboratory facilities and/or their time in securing funds and logistical requirements. I was the senior author on all papers presented in this thesis and was responsible for the organisation and execution of all field seasons, laboratory and data analysis and the preparation of publications. However, several co-authors have contributed significantly to some of the chapters. Dr Yves Cherel (CEBC-CNRS, France) verified the identification of otoliths and squid beaks retrieved from scat samples and supplied their measurements (Chapter 4); Laurent Dubroca (CEBC-CNRS, France) extracted the environmental data referred to in Chapters 5&6 and also constructed the time spent diving per sector plots in Chapter 6; and Professor Guy Duhamel and Patrice Pruvost of the Natural History Museum in Paris conducted transect surveys of myctophid abundance on board '*La Curieuse*' and identified and measured the samples discussed in Chapter 6.

Chapter 2

Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Îles Kerguelen

2.1 Introduction[1]

The diving behaviour of marine predators, quantified by the use of time-depth recorders (TDRs), is one of the most commonly used measures for differentiating foraging activity between individuals and populations both spatially and temporally (Antonelis *et al.* 1990; Hindell *et al.* 1991; Schreer and Testa 1996; Bowen *et al.* 1999; Cherel *et al.* 1999; Bonadonna *et al.* 2000; Georges *et al.* 2000a and b). In recent years the diving behaviour of several marine predators has also been linked to spatial and temporal variability in the availability of prey species (Boyd *et al.* 1994; Bost *et al.* 1997; Swartzman and Hunt 2000; Guinet *et al.* 2001). Individual predators exploit prey resources and respond to environmental variability in different ways. These 'strategies' may vary in relation to prey availability, an individual's age and experience in terms of locating prey, and physiological limits associated with diving capabilities.

Antarctic fur seals, *Arctocephalus gazella*, are one of the most widely studied marine predators, both in terms of life history and foraging ecology. Studies of their foraging ecology have been investigated across their range in the Southern Ocean, from South Georgia (Boyd and Croxall 1992; McCafferty *et al.* 1998), Macquarie Island (Goldsworthy *et al.* 1997), Heard Island (Green *et al.* 1997; Green 1997), the Kerguelen Archipelago (Bonadonna *et al.* 2000; 2001; Guinet *et al.* 2001) to the South Shetland Islands (Costa *et al.* 2000; Goebel *et al.* 2000) and the South Orkney Islands (Daneri and Coria 1992; Daneri and Coria 1993). The breadth of data now currently recorded on the foraging behaviour of this species is one of the most comprehensive of any marine predator, revealing a flexibility in prey choice and foraging strategies between different localities and/or in relation to variability in the marine environment.

At some localities, such as South Georgia, Antarctic fur seals feed primarily on krill, with fish comprising an important part of the diet in winter, spring and during the breeding season in some years (North *et al.* 1983; Reid 1995; North 1996; Reid and Arnould 1996). However, conspecifics at other sites, such as Marion, Macquarie and Heard Islands and the Kerguelen Archipelago feed on a more diverse range of meso-pelagic fish prey, primarily, myctophid and notothenioid fish, and cephalopods (Cherel *et al.* 1997; Goldsworthy *et al.* 1997; Green *et al.* 1997). The distribution of some species of myctophid in the Southern Ocean is related to the position of the Antarctic Polar Front (PF) (Sabourenkov 1991), which varies considerably between years in the vicinity of the Kerguelen Plateau (Moore *et al.* 1999a). Thus, variation in the diving behaviour of marine predators in response to

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fluctuations in prey availability in association with movement of the PF, if they occur, are likely to be detected in the Kerguelen region.

Recent studies have identified considerable inter-population variation in diving behaviour which is often attributed to these large scale differences in prey type, distribution or abundance, linked to differences within the marine environment (McCafferty *et al.* 1998; Goebel *et al.* 2000; Guinet *et al.* 2001). However, these factors may also operate at smaller spatial and temporal scales (Guinet *et al.* 2001), and may result in variation in diving behaviour even within a colony. As central place foragers (Orians and Pearson 1979), lactating Antarctic fur seals are limited in their exploration of the marine environment whilst foraging by the fasting capabilities of their pups. Individual differences in diving behaviour, which are thought to reflect foraging activity (Boyd *et al.* 1994), and consequently foraging efficiency (in terms of pup provisioning rates), may ultimately confer individual advantages in terms of breeding success.

In 1994, Boyd *et al.* hypothesised that variation in foraging patterns between seals within years may be attributed to individual differences in foraging strategies, while differences between years are attributable to changes in prey abundance. Here, we describe the classification of behavioural diving 'strategies' of female Antarctic fur seals, not previously studied, at Îles Kerguelen. We aim to identify intra- population variability in diving behaviour over three years, and between seasons, on the basis of a range diving parameters, using an objective clustering and multi-dimensional scaling techniques.

2.2 Materials and methods

2.2.1 Study site

Lactating Antarctic fur seals were studied at the Kerguelen Archipelago (Fig. 2.1) during the austral summers of 1997/98 (Feb.-Mar.), 1998/99 (Dec.-Mar.) and 1999/00 (Dec.-Mar.), hereafter referred to as 1998, 1999 and 2000 respectively. The seals at Cap Noir, a colony with approximately 800 breeding females situated on the north-eastern coast of the Courbet Peninsula (49°07'S, 70°45'E), formed the basis of the study. Antarctic fur seals breeding on Île de Croy, Îles Nuageuses (48°38'S, 68°38'E), located to the north west of the archipelago, were also studied in January 2000. This colony comprises approximately 4000 breeding females (Guinet *et al.* 1996).

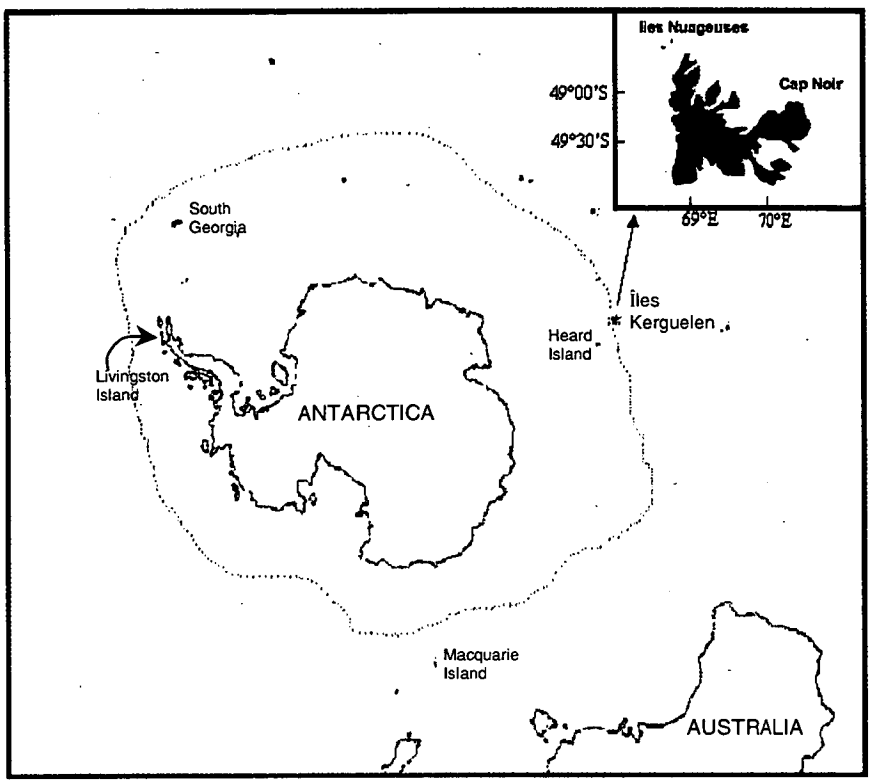

Figure 2.1 Location of the study sites at Îles Kerguelen, southern Indian Ocean, and other sub-Antarctic breeding sites of Antarctic fur seals.

2.2.2 Data collection

During the three years, 129 time-depth recorders were deployed on females (TDRs, Wildlife Computers, Redmond, Washington, USA), 117 of which provided successful dive records. Three seals returned without units, one seal left the colony with her pup before the unit could be retrieved, and in seven instances the Mk7 TDR failed to record dive data. Sixteen of the dive records were collected with either a single MK7 TDR (n=7) attached anterior to the tail or a MK5/PTT combination (n=6) attached between the scapulae of female seals, at Île de Croy, Îles Nuageuses in January 2000. Fifteen TDRs were recovered with 13 providing data. Seals were captured ashore using a hoop net and were subsequently weighed, a standard length measurement recorded (nose to tail) and an individual number applied to the fur on the rump with peroxide hair-dye (Bristol Myers-Squibb, Rydalmere, Australia). During the attachment of the devices, adult seals were held on a wooden restraint board. Four types of TDR were used during the study (Table 2.1). In 1998, MK6 Velocity TDRs or MK5 TDR/PTT units (Bonadonna *et al.* 2000) were attached dorsally to the fur between the scapulae using two-part Araldite (AW 2101, Ciba Specialty Chemicals, Switzerland). In 1999 and 2000 MK7 TDRs replaced MK5 TDRs, and were attached dorsally in conjunction with a PTT, or singly, 10cm anterior to the base of the tail.

Table 2.1: Summary of TDR deployments on Antarctic fur seals at Îles Kerguelen (1998-2000).

Year/season		Type of TDR			
		Mk6	PTT/Mk5	PTT/Mk7	Mk7
1998	late	10	12	0	0
1999	early	0	0	9	8
	late	5	0	9	3
2000	early	0	6	10	22
	late	1	0	12	10
Total		16	18	40	43

Once TDRs were retrieved, data were downloaded directly to a portable laptop computer during the post-foraging attendance period after one (n=101), two (n=14) or three (n=2) trips to sea. Only data recorded during the first trip to sea (n=117) were used in this study, which included data from five individuals in two consecutive years. Mk5 and MK6 records were extracted with 3-M software (Wildlife Computers), while Mk7 records were converted from hexadecimal format to decimal format with Hexdecode software (Wildilfe Computers). Offset and drift of the pressure transducers were corrected using customised software (DiveView, Bryan Dumsday) in LabView 4.0 (National Instruments Corp., Austin, TX, USA). The depth resolution of TDRs was ±1m, except in the case of 10 Mk6 records for which it was ±2m. Only dives ≥4m (double the depth resolution of the least sensitive units) were included for all TDR records. Basic dive parameters (see below) were extracted from the decimal files using customised software (DIVE, Stewart Greenhill).

All TDRs were programmed to record depth every 5s. Mk5 and Mk6 TDRs were returned with full memories in 13 instances. The arrival time of these seals was calculated as the mid point between successive observational checks of the colony for maternal attendance, which were conducted at approximately 0800 and 1900 each day.

2.2.3 Bout analyses

An iterative statistical technique based on that used by Boyd *et al.* (1994) and modified by Harcourt *et al.* (2001) identified bouts of diving. Minimum criteria for inclusion as a bout were three dives greater than six metres depth within a 20-minute period (Boyd and Croxall 1992; Boyd *et al.* 1994) in order to exclude traveling dives. Once the minimum bout criteria were satisfied, the duration of the subsequent surface interval was compared to the upper 95% confidence limit of the mean surface interval within the bout. Subsequent dives were included if the surface interval was less than the mean value, which was recalculated after the inclusion of each additional dive. The bout was considered to have ended once the proceeding surface interval exceeded the recalculated confidence limit (Boyd *et al.* 1994; Harcourt *et al.* 2001).

In order to test whether or not the observed bout pattern represented structured behaviour, rather than random distribution of dives, the dives were randomised and the bout analysis was run again. This process was repeated 1000 times per dive record. If the number of bouts detected per replicate was greater in the random scenario than in the actual dive record in more than 95% of cases then the dive record was considered to have bout structure (Harcourt *et al.* 2001).

2.2.4 Diving parameters

Twelve parameters were derived from the diving record of each foraging trip: (1) diving frequency (number dives h^{-1}); (2) nightly diving frequency (number of dives h^{-1} of night); (3) mean depth (m); (4) mean dive duration (s); (5) proportion of time spent submerged (sum of duration of dives greater than 4m depth, to exclude traveling behaviour), expressed as proportion of total trip duration (%); (6) proportion of night-time spent submerged (%); (7) trip duration (days); (8) proportion of dives in bouts (%); (9) number of dives per bout; (10) number of dives at night as proportion of all dives (%); (11) vertical depth travelled per hour of night (two times the sum of nightly dive depth divided by number of night hours); and (12) proportion of total vertical depth dived at night (%).

Many of the diving parameters, such as trip duration, mean depth and duration and time spent diving have been used commonly in other studies of otariid diving behaviour (e.g. Arnould *et al.* 1996a; Georges *et al.* 2000b). Preliminary exploration of the dive data also

indicated that for some seals, diving during the day constituted a considerable proportion (up to 67.2%), of the duration of the foraging trip. Consequently, we have included several variables quantifying the extent of daytime diving *i.e.* proportion of dives occurring at night, proportion of total vertical depth at night and proportion of night-time spent submerged. All means are expressed as ± standard deviation.

The duration of day and night periods was calculated based on sunrise and sunset times for Cap Noir (AUSLIG software, Department of Industry Science and Resources, Canberra, Australia). The duration of night ranged from 7.8 to 11.5 hours during the course of the study. Each dive record was also assigned a seasonal classification of either (1) early summer for deployments from 15 December to 19 January or (2) late summer for deployments from 20 January to 15 March.

2.2.5 Statistical analysis

2.2.5.1 Quantification of differences in dive behaviour

Multidimensional scaling and cluster analysis (MDS) is an exploratory or an hypothesis generating procedure, conducted without any assumptions of the distribution of variables (Belbin 1985). Given the lack of previous information concerning the diving behaviour of marine predators in the Kerguelen region and the large sample for which diving behaviour was collected during this three year study, clustering and MDS techniques provided a suitably objective way of categorizing the differences in diving activity of individual females both across and between years.

The seals were allocated to behavioural groups on the basis of the variables outlined above. Dive records from both study colonies were included in order to encompass as large a range of diving behaviours as possible for the Kerguelen region. The 12 dive parameters for each individual dive record were included in both a cluster and an MDS analysis. A Canberra Metric association matrix was employed to construct a dissimilarity matrix (Belbin 1993) primarily on the basis of its suitability for proportional data and as it performed highly in a comparison of 11 similarity measures (Cao *et al.* 1997). The Unweighted Pair Group arithMetic Averaging (UPGMA) clustering algorithm was then applied to the dissimilarity matrix (Belbin *et al.* 1992), and non-hierarchical agglomerative fusion strategy was then used to group similar seals and produce a dendrogram. Finally, Semi-Strong-Hybrid multi-dimensional scaling (Belbin *et al.* 1992) was used to enable the visualisation of the relationship between groups in three-dimensions.

A backwards discriminant function analysis using SYSTAT® 9 (SPSS Inc.) was conducted to determine the accuracy of assigning seals to a particular dive group. A jackknife analysis was then used to verify the accuracy of the DFA (Tabachnick and Fidell 1996).

2.2.5.2 Variability in dive group distribution

We tested for seasonal (early and late) and inter-annual (1998, 1999, 2000) differences the behavioural groups for seals from Cap Noir only using the Log Likelihood Goodness of Fit test (Sokal and Rohlf 1995). The G-statistic was compared to critical vales of the Chi-squared distribution (Rohlf and Sokal 1995). Only dive records for individuals equipped with PTTs in late summer were included in inter-annual comparisons as no data were collected in early summer 1998 and to reduce any bias associated with deployment type. A detailed comparison of the diving behaviour and foraging ecology between *A. gazella* females breeding at Îles Nuageuses and Cap Noir will be conducted in an upcoming paper.

2.3 Results

2.3.1 General diving behaviour

A total of 188 016 dives made during 117 foraging trips by 111 seals from both colonies were analysed. The maximum depth attained by any seal was 240m during a dive lasting 5.3 minutes in January 2000 (Table 2.2). The maximum depths and dive durations for individual seals ranged from 117-240 m and 2.5-5.3 min. respectively (Appendix). The mean dive depth recorded for all seals was 53±17 m and mean dive duration was 1.6±0.4 minutes. The average depths to which the seals dived on foraging trips varied considerably between individuals and ranged between 16m and 113 m. On average, 87.5 ± 13% of dives occurred at night. A diurnal pattern in diving activity and diving depth was evident for many seals with deeper dives often occurring around dawn and dusk, and a higher proportion of seals diving between these times (Fig. 2.2*a*). The total time spent diving to greater than 4m during a foraging trip also varied considerably between individuals (8-37%, $\bar{x}$ =22.5%, Fig. 2.2*b*) and was negatively correlated to foraging trip duration (r^2=0.14, P<0.001, Fig 2.2*c*).

Table 2.2: Average diving behaviour of Antarctic fur seal females foraging at Îles Kerguelen (n=117 trips).

Diving parameter	Mean	SD	Minimum	Maximum
Dives per hour (hr^{-1})	9.1	2.8	3.9	20.8
Dives per hour of night	22.2	7.7	7.7	47.3
Mean depth (m)	53	17	16	113
Mean duration (min)	1.6	0.4	0.5	2.6
Time spent diving (%)	22.5	5.0	8.1	37.2
TSD at night (%)	50.1	10.3	19.3	70.0
Trip length (d)	7.4	3.1	2.7	17.9
Proportion of dives in bouts (%)	94.4	5.4	61.9	99.8
Number of dives per bout	10.7	1.7	8.2	16.6
Number of dives at night (%)	87.5	13.1	32.8	99.8
Depth per hour of night (m hr^{-1})	1956	473	838	3020
Vertical depth at night (%)	80.7	18.3	19.6	99.9

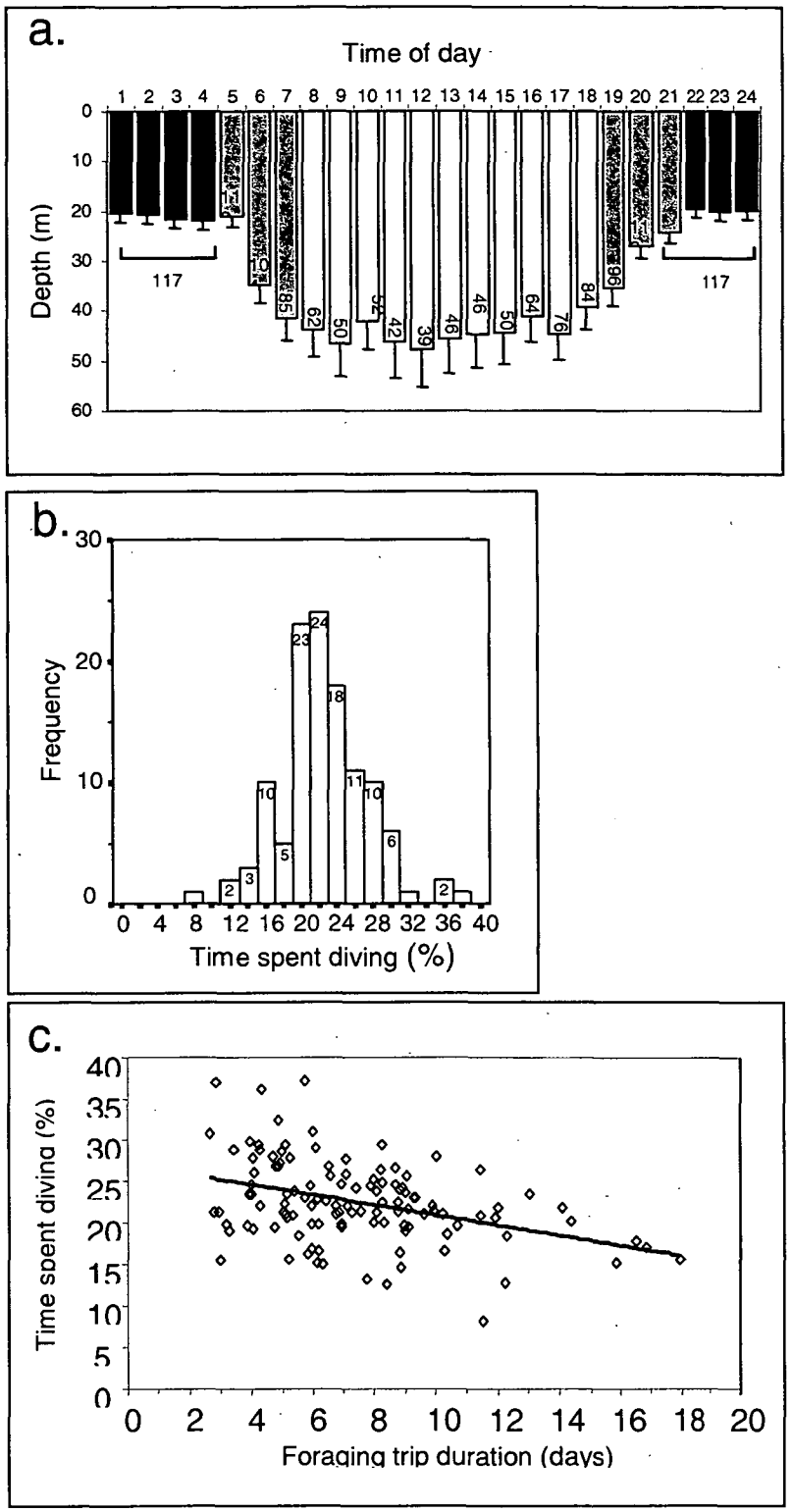

Figure 2.2 (a) Maximum dive depth of Antarctic fur seals at Iles Kerguelen in relation to time of day (error bars denote one standard error, sample sizes are noted in or above bars); *(b)* frequency histogram of time spent diving during a foraging trip (n=117); (*c*) the relationship between time spent diving and foraging trip duration.

Bout structure was observed in the diving behaviour during 115 foraging trips, as shown by a greater number of bouts in the randomizations as opposed to the observed situation. Bouts occurred in the randomized situation in 76 and 87% of the cases for the other two seals (K8_00 and S2_00). After visually inspecting the two records, and given the high proportion of seals displaying bout behaviour, we decided to include the bout statistics for K8_00 and S2_00. The proportion of dives occurring in bouts ranged from 61.9-99.8%. The seals averaged 10.7 dives per bout (Table 2.2) and an absolute rate of 9.1 dives per hour, or 22.2 dives per hour of night.

2.3.2 Behavioural dive groups

A dendrogram of the dissimilarity in diving behaviour between the 117 foraging trips, based on the cluster analysis, indicated four Behavioural Dive Groups (BDG): (1) Deep (n=60); (2) Shallow/active (n=45); (3) Shallow (n=9) and (4) Daytime (n=3) divers. Groups were clearly identified by MDS with the ordination of the data in three dimensions yielding 4 discrete groupings with acceptably low stress value of 0.09 (Fig. 2.3).

The difference in dive behaviour between the four groups in relation to time of day is displayed in Figure 2.4. The 'deep' diving seals sustained greater depths on average (63m) than other seals and spent 24% of their time at sea diving (Table 2.3). Seals in the 'shallow-active' BDG2 spent a similar proportion of their time at sea diving (22.2%). Seals in this group dived on average to only 41m depth and dived at the highest rate (11.1 dives per hour). The 'shallow' diving seals of BDG3 can be distinguished from the shallow-active seals in BDG2 by the reduced amount of time spent diving (14.5%) although seals were diving to similar mean depths (36m). Seals in this group also recorded the lowest proportion of dives in bouts (82%) and the lowest number of dives per bout (9.5). Only three seals displayed the daytime diving typical of BDG4 (see Appendix). Time spent diving at night was particularly low for these seals with only 59% of dives occurring at night.

The morphological characteristics of the female seals in terms of length (cm) and mass (kg) did not vary as a function of behavioural dive group when tested by ANOVA. (Length: $F_{3,116}=0.516$, $P=0.671$; Mass: $F_{3,116}=1.064$, $P=0.367$). Examples of diving records for seals from each of the diving categories are shown in Figure 2.5.

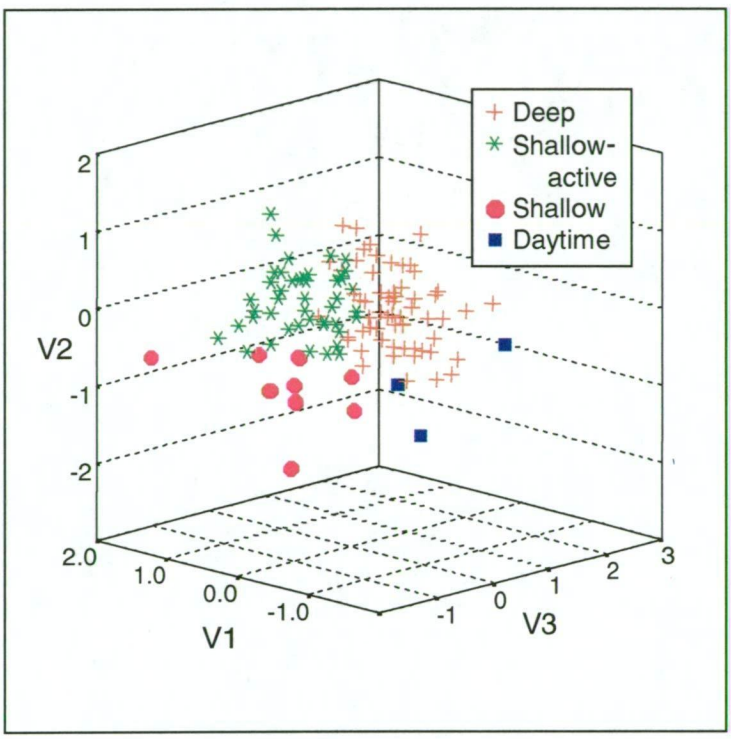

Figure 2.3 Behavioural dive groups of female Antarctic fur seals as produced by multidimensional scaling and plotted in three dimensions.

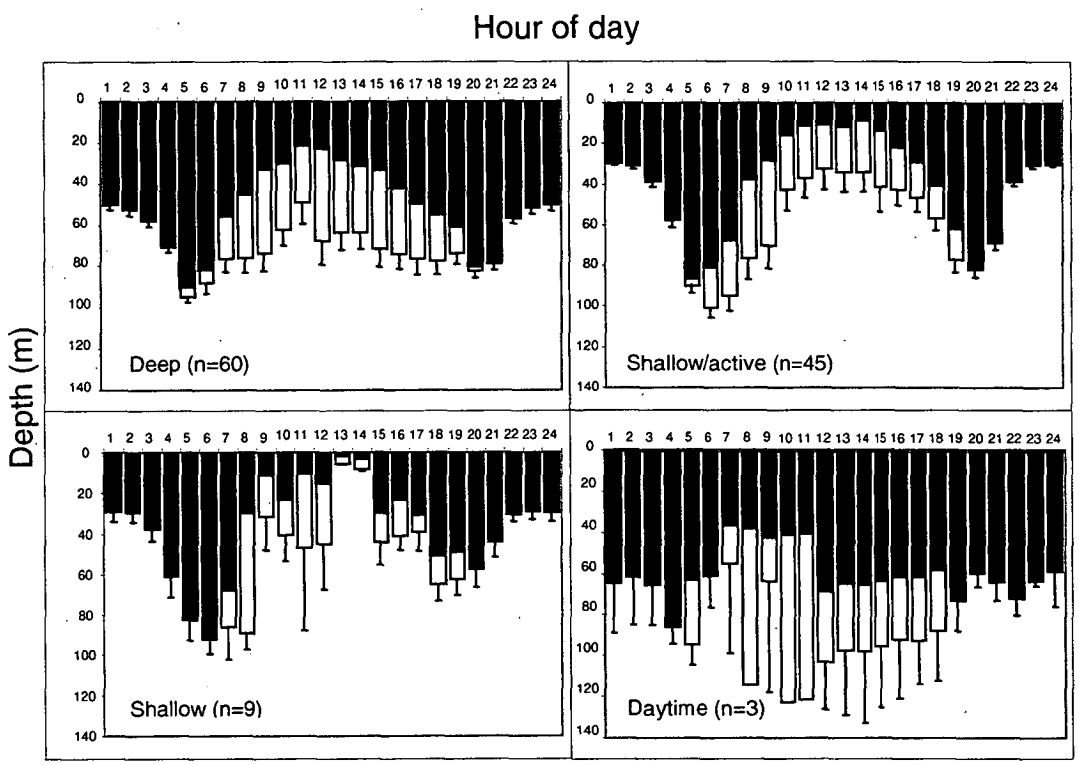

Figure 2.4 Mean dive depth of seals in the four behavioural dive groups in relation to time of day. Black bars depict the proportion of seals per group diving in a particular hour (a full black bar indicates 100% of seals dived in that hour). Error bars are + 1 SE.

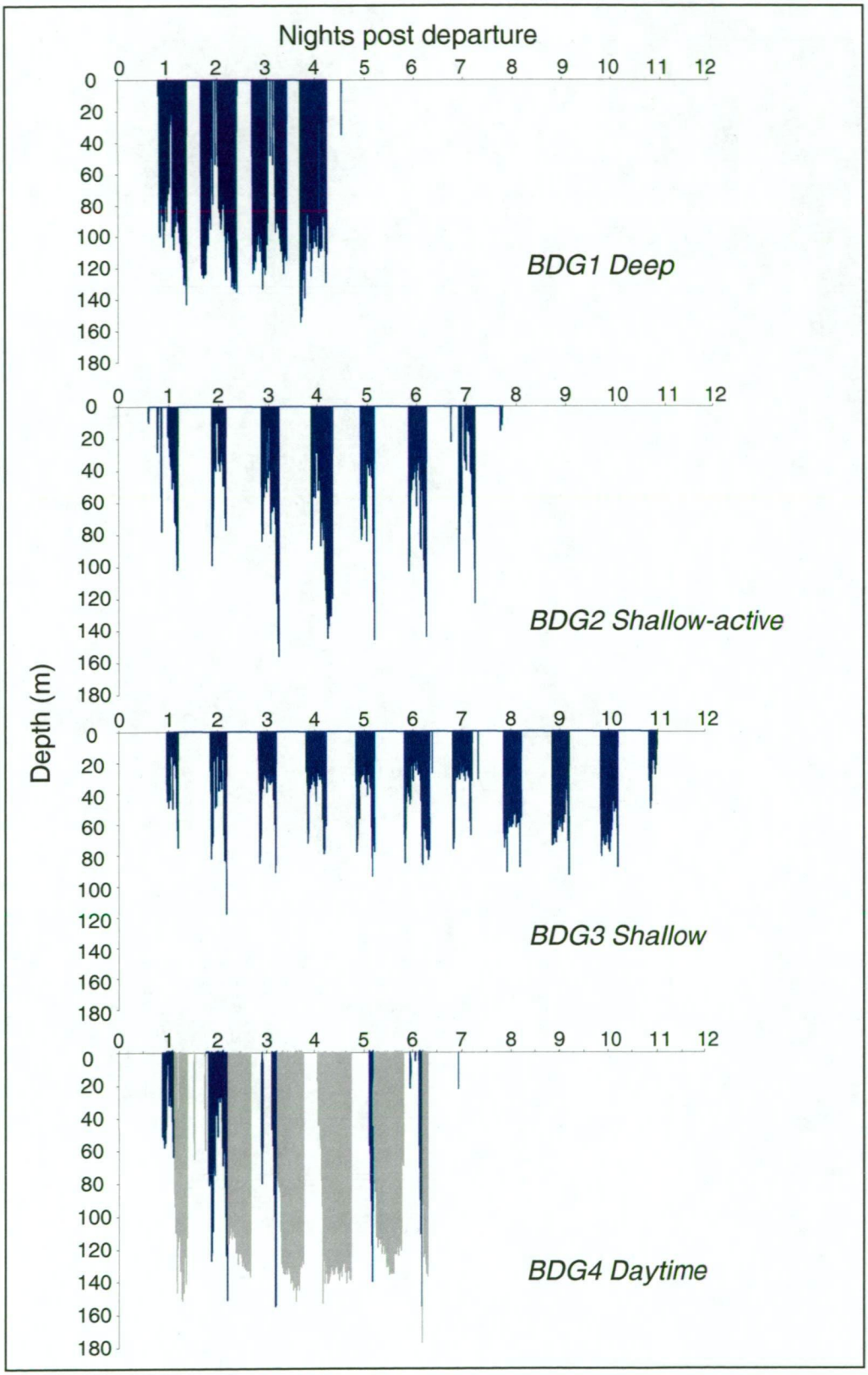

Figure 2.5 Diving records plotted in two-dimensions of four female Antarctic fur seals assigned to: (*a*) the deep behavioural dive group (BDG) 1; (*b*) the shallow-active BDG2; (*c*) the shallow BDG3; and (*d*) the daytime BDG4 (daytime dives in grey).

A backwards DFA was conducted for seals in BDG 1, 2 and 3. Seals in BDG 4 accounted only for 2.5% of the population and were excluded due to low sample size (1.7% from Cap Noir and 0.8% Îles Nuageuses, see Appendix). The DFA correctly assigned 94% of seals to behavioural diving groups using 10 of the 12 diving parameters (daytime divers excluded). Cross-validation using a jackknife analysis found 96% of the seals to be correctly assigned. The two diving parameters removed from the analysis were those largely responsible for the distinction between daytime diving seals (proportion of time spent diving at night and the percentage of dives occurring at night).

Table 2.3: Summary statistics of diving parameters for four behavioural dive categories as identified by clustering.

Diving parameters	Behavioural Dive Group			
	1 Deep	2 Shallow-active	3 Shallow	4 Daytime
N	60	45	9	3
Length (cm)	116.8 ± 5	115.3 ± 5	117.1 ± 4.1	117.7 ± 5.1
Maternal mass (kg)*	32.4 ± 4.0	31.5 ± 4.6	31.1 ± 3.5	31.9 ± 1.4
Dives per hour (hr^{-1})	7.8 ± 1.6	11.1 ± 2.4	9.2 ± 4.6	6.2 ± 2.0
Dives per hour of night	17.9 ± 3.5	29.1 ± 5.7	21.9 ± 10.3	8.1 ± 0.7
Mean depth (m)	63 ± 15	41 ± 7	36 ± 11	76 ± 15
Mean duration (min)	1.9 ± 0.3	1.2 ± 0.2	1.1 ± 0.3	2.0 ± 0.2
Time spent diving (%)	24.1 ± 4.9	22.2 ± 3.6	14.5 ± 2.9	20.1 ± 7.1
TSD at night (%)	51.1 ± 8.7	53.9 ± 7.0	32.6 ± 6.6	25.9 ± 2.9
Trip length (d)	6.2 ± 2.4	7.7 ± 2.6	13.1 ± 3.8	8.8 ± 2.5
Proportion of dives in bouts (%)	95.9 ± 2.2	94.9 ± 4.3	82.3 ± 9.4	91.9 ± 5.1
Number of dives per bout	11.0 ± 1.7	10.6 ± 1.6	9.5 ± 0.9	9.9 ± 1.1
Number of dives at night (%)	84.0 ± 13.9	92.9 ± 5.5	92.4 ± 6.6	59.0 ± 33.4
Depth per hour of night ($m\ hr^{-1}$)	1977 ± 492	2105 ± 314	1362 ± 317	1088 ± 203
Vertical depth at night (%)	77.4 ± 20.7	85.4 ± 11.9	87.1 ± 9.6	57.1 ± 38.6

*mean value of maternal mass at deployment and retrieval of the TDR, N = no. of trips

The canonical scores clearly distinguishing the three dive groups are plotted in Figure 2.6. The first discriminant function accounted for 72.4% of the between group variability, while 27.6% was accounted for by the second.

2.3.3 Variability in behavioural dive group distribution

2.3.3.1 Season

No difference in the diving behaviour of seals between early and late summer was apparent in either 1999 or in 2000 (Fig. 2.7*a* and *b*).

2.3.3.2 Colony

No significant difference between the types of diving behaviour of seals at Îles Nuageuses (n=12) and at Cap Noir (n=25) was evident in early lactation 2000 ($G=4.12<\chi^2_{2,0.05}$). However, there appeared to be a higher proportion of shallow/active diving seals at Cap Noir (Fig. 2.7*c*).

2.3.3.3 Year

A comparison of the proportion of seals fitted with PTTs assigned to BDGs in late summer indicated a highly significant difference in the frequency distribution of dive groups between years ($G=10.05>\chi^2_{4,0.05}$). This appears to be due to a shift from the high proportion of deep diving seals in 1998 to a more even distribution between these two diving behaviours in 2000 (Fig. 2.7*d*). Of the five seals studied in consecutive years, four seals were assigned to the same BDG in both years (BDG1 n=3, BDG2 n=1) and one seal was assigned to BDG3 in 1998 and BDG1 in 1999.

2.4 Discussion

The range in diving activity recorded for lactating Antarctic fur seals at Îles Kerguelen in this study confirms previous observations of the flexibility of foraging strategies for this species (McCafferty *et al.* 1998; Boyd 1999). Most seals displayed shallow, nocturnal diving activity with deeper crepuscular dives, characteristic of fur seals preying on pelagic species (Boyd and Croxall 1992; Goldsworthy *et al.* 1997). However, considerable intra-population variation was evident on the basis of several diving parameters, particularly, the proportion of vertical depth attained at night, the proportion of time spent diving overall and at night, and the number of dives per hour or per hour of night. For example, three seals (two in 1998 and one in 2000) conducted a high proportion of dives during daytime, while most seals only dived at night.

2.4.1 Behavioural dive groups

Although much inter-individual variation in dive behaviour was apparent, our analyses revealed four broad diving categories or strategies. Some individual variation within the groups may be due to factors such as TDR type, however it is difficult to account for such effects given the multi-year, multi-season and multi-site nature of the data.

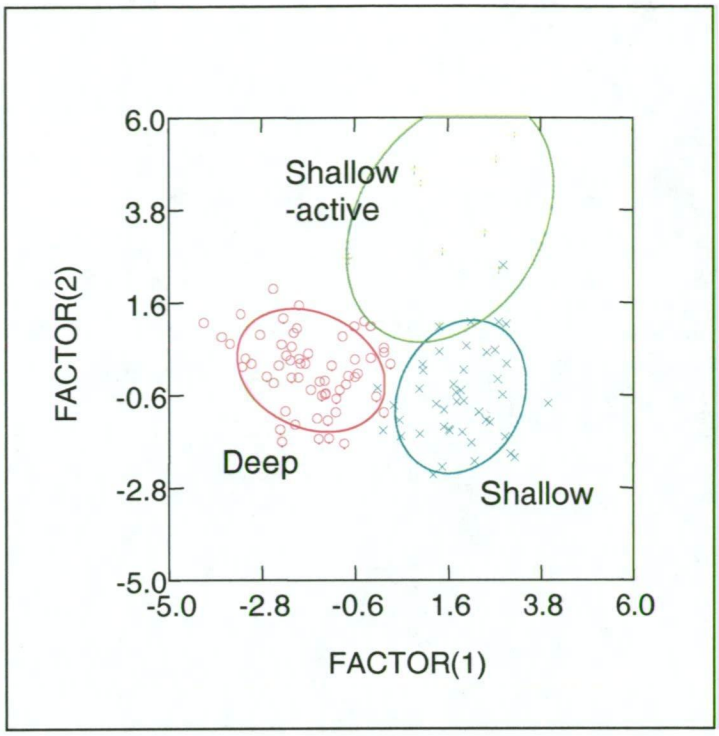

Figure 2.6 The canonical scores plot for seals in the deep (n=60), shallow-active (n=45) and shallow (n=9) behavioural dive groups.

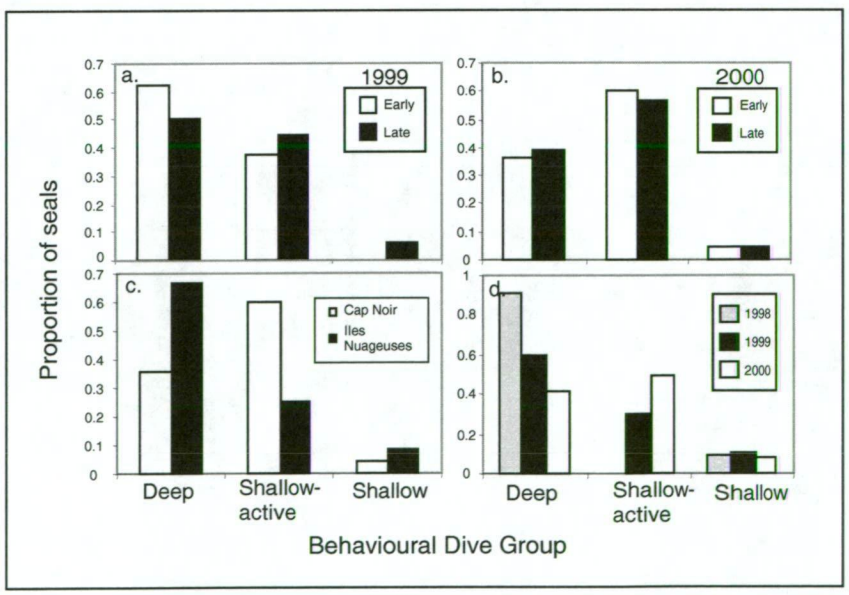

Figure 2.7 (*a-d*)The frequency distribution of Antarctic fur seals assigned to three diving activity categories (*a*) 1999 seasonal comparison, (*b*) 2000 seasonal comparison and (*c*) inter-site comparison between Cap Noir and Iles Nuageuses in early summer 2000 and (*d*) inter-annual comparison (1998-2000).

2.4.1.1 BDG1 - Deep divers

The majority of dive records (51.2%) were assigned to the deep-diving behavioural group. These seals dived to both deeper absolute (240m) and mean depths (39-113m, $\bar{x}$= 63m) at the Kerguelen Archipelago than at any other site where the diving behaviour of female Antarctic fur seals has been studied (Table 2.4). Female seals at Heard Island (Green 1997), also positioned on the Kerguelen Plateau, are the only population of Antarctic fur seals reported to display mean diving depths (10-47m) approaching those of the seals in this study. It is possible the shallow mean dive depth (13m) of Antarctic seals studied at Bird Island (McCafferty *et al.* 1998) could be explained by the lower minimum dive depth criterion of ≥1m (Table 2.4). Approximately 68% of dives over the three years of our study were ≤4m. If an equivalent proportion of 1m dives are incorporated into the mean diving behaviour of the 117 seals in this study (Table 2.2), a dive depth of 18m is obtained. However, while dive depths of 1-2m may represent foraging by seals on surface swarming krill at South Georgia, shallow dives at Kerguelen (in the absence of krill swarms) would likely represent either pressure transducer variability, given the resolution of some TDRs, and/or surface traveling dives. In addition, nocturnal trawls conducted for myctophids in the vicinity of Kerguelen by Duhamel *et al.* (2000) indicated high abundances of species preyed upon by Antarctic fur seals occurring well below the surface at 50m.

On average, seals in BDG1 also conducted shorter foraging trips than other seals, and while the majority of dives were conducted at night, more daytime dives were recorded than for the more shallow diving seals. Given the large proportion of dives in bouts (96%), the relatively short duration of foraging trips and the consistent nocturnal diving rate (18 dives hr^{-1} of night) of deep diving seals at Kerguelen, it is probable that these seals were travelling to a relatively constant or reliable, pelagic food source, which could only be accessed at considerable depth. Antarctic fur seals foraging over the continental shelf near Cape Shirreff, Antarctica, were found to dive deeper with a higher proportion of daytime dives than those diving on the shelf break or over deep water (Goebel *et al.* 2000). The diving patterns of Northern fur seals, *Callorhinus ursinus*, studied at St Paul Island also separated primarily on the basis of depth. Deep divers expended less energy diving than shallow divers, while apparently obtaining greater energy per dive (Goebel *et al.* 1991). Deep-diving Northern fur seals fed principally on benthic fish species over the continental shelf (Goebel *et al.* 1991), whilst the majority of seals tracked at Cap Noir concentrated their foraging activity in waters greater than 500m on the edge of the Kerguelen Plateau (Guinet *et al.* 2001). Chapters 5 and 6 will focus on the relationship between diving strategies, location at sea and the foraging success in terms of pup provisioning of individual seals.

Table 2.4: Inter-population comparison of diving activity for Antarctic and Northern fur seals at various sites.

Species	Year	n	Mean Depth (m)	Trip length (d)	TSD (%)	Diet	Dive criterion
Antarctic fur seal							
Îles Kerguelen [a]							
Deep		60[t]	63	6.2	24.1	F+S [j]	≥ 4m
Shallow/active		45[t]	41	7.7	22.2	F+S	≥ 4m
Shallow		9[t]	36	13.1	14.5	F+S	≥ 4m
Daytime		3[t]	76	8.8	20.1	F+S	≥ 4m
Mean		117[t]	53	7.4	22.5	F+S	≥ 4m
South Georgia	88/89-89/90 [b]	11	8-19*	2.5-8	13.6	K	≥ 2m
	1994-96 [c]	385[t]	12.7	4.5	34^	K	≥ 1m
Heard Island [d]	1992	3	13.2	-	-	F+S	≥ 5m
	1993	9	36.1	-	-	F+S	≥ 5m
Macquarie Island [e]	1991	14	12±11	2.5	10.4	F+S	> 2m
Cape Shirreff	1998 [f]	11	13.3-20.6	4.6	-	K + F	≥ 4m
	1998 [g]	14	19	4.54	9.8	K, F, F+K	≥ 4m
Northern fur seal							
St Paul Island [h]							
Deep		4	84.5	-	-	F+S	-
Shallow		5	43.7	-	-	F+S	-
St George Island [i]	1980,1982	7	68	7.5	-	F+S	-

t n = number of trips; * median value; ^ time spent diving calculated for trip duration excluding transit times; F - fish, S - squid and K - krill. Time spent diving (TSD) is interpreted as the amount of time spent submerged.
a This study; *b* Boyd and Croxall 1992; *c* McCafferty *et al.* 1998; *d* Green 1997; *e* Goldsworthy *et al.* 1997; *f* Goebel *et al.* 2000; *g* Costa *et al.* 2000; *h* Goebel *et al.* 1991; *i* Gentry *et al.* 1986; *j* Cherel *et al.* 1997.

2.4.1.2 BDG2 – Shallow-active divers

Seals diving shallowly and more actively (n=40) conducted the majority of their dives at night. Mean dive depths, while still deeper than for most populations of Antarctic fur seals, were shallow for seals breeding at Kerguelen, ranging from 25 to 54m. This pattern of diving with relatively elevated rates of time spent diving and vertical depth travelled per hour of night is consistent with dive behaviour noted for other populations of Antarctic fur seals at *e.g.* Macquarie Island where seals also feed primarily of myctophid fish and at South Georgia where seals feed primarily on shallow schooling krill (Reid and Arnould 1996).

2.4.1.3 BDG 3 - Shallow divers

The overall and nightly proportion of time spent diving by seals in BDG3, 14.5 and 32.6% respectively, was low in comparison to the other shallow diving seals of BDG2 (23.2 and 53.9% respectively). In addition to the reduced proportion of dives in bouts and number of dives per bout for this group, it appears that seals may be spending a higher proportion of their time at sea searching for prey and/or feeding on a less aggregated prey source than more active, shallow diving seals of BDG2.

Arnould *et al.* (1996a) found a close negative sigmoidal relationship between at-sea metabolic rate and the proportion of time at sea spent diving in a study of the at-sea metabolism of female Antarctic fur seals at Bird Island, South Georgia. The authors suggested the measure (time spent diving) could provide a useful and inexpensive estimate of energy expenditure. At-sea metabolism was not measured at Îles Kerguelen, however the reduced proportion of time at-sea spent diving for this group may reflect a higher metabolic rate for these seals. Costa *et al.* (2000), in a study of the foraging energetics of Antarctic fur seals at Livingston Island, found no such relationship and suggested that the high field metabolic rates recorded were due to a large proportion of surface swimming as only 10% of time at sea was spent diving.

Based on the findings of Arnould *et al.* (1996a) and Costa *et al.* (2000) we hypothesise that seals in BDG3 had higher FMR than other seals, due in part to higher levels of surface swimming while searching for prey patches (see Bonadonna *et al.* 2000).

2.4.1.4 BDG 4 - Daytime divers

This small group representing 2.5% of foraging trips studied, included a high proportion of daytime dives to average depths far greater than those for other groups. We may have expected these seals to be larger in terms of length and mass as a direct relationship exists between the diving capability of a marine mammal and its metabolic stores (Kooyman 1989 in Costa *et al.* 2000; Hindell *et al.* 1992). However, no difference in size was found between seals in the different behavioural dive groups. This may be due in part to the low numbers of seals (n=3) exhibiting this particular behaviour.

Few studies have examined longitudinal trends in the foraging strategies of fur seals. McCafferty *et al.* (1998) observed female identity to be important in explaining variation in foraging trip duration and in diving activity of Antarctic fur seals at Bird Island, while at Îles Kerguelen, Bonadonna *et al.* (2001) found the direction taken by seals fitted with satellite transmitters during consecutive foraging trips to be similar. Of the small number of seals studied in consecutive years in this study, 80% were assigned to the same behavioural dive group in both years, highlighting the importance of longitudinal studies in examining foraging strategies.

2.4.2 Inter-population comparisons of dive behaviour

It is apparent that the diving activity of seals in the Kerguelen region differs from that of conspecifics at other sites (see Table 2.4). Unfortunately quantitative comparisons of diving behaviour between sites are hindered by differences in both methodology (TDR types and sampling protocols) and analysis techniques. For example, the lower minimum depth

criterion of many studies will reduce the average dive depth recorded for these seals. However, some general patterns are apparent, particularly that seals at Îles Kerguelen dive more deeply while making longer foraging trips than do seals from other populations, such as at Macquarie (Goldsworthy *et al.* 1997) and Heard Islands (Green 1997), where seals feed on similar prey. In many respects the diving activity of *A. gazella* females at Kerguelen differs from the diving behaviour of krill feeding Antarctic fur seal populations, and in fact appears more similar to that of Northern fur seals, the Arctic counterpart of Antarctic fur seals (Table 2.4). The higher incidence of consistently deep diving behaviour at Îles Kerguelen than at other breeding sites, particularly in 1998, raises questions about the prey availability and variability of the marine environment around the Archipelago. Examination of the relationship between behavioural dive groups and the spatial utilisation of the marine environment by seals should further clarify the ecological significance of the dive groupings.

Georges *et al.* (2000b) studying Sub-Antarctic fur seals, *Arctocephalus tropicalis*, at Amsterdam Island, observed that seals exhibited markedly different diving behaviour between the first trip after parturition, in summer, and in winter. Seals increased their time spent diving in winter, diving to greater depths, indicating a greater diving effort was required at this time. Maternal foraging efficiency in winter decreased in comparison to earlier months (Georges and Guinet 2000) implying lower prey availability in winter (Georges *et al.* 2000a).

Seasonal differences in diving behaviour were not observed at Îles Kerguelen. The lactational period of Antarctic fur seals (4 months) is relatively short in comparison to that of Sub-Antarctic fur seals (10 months), which forage further from their colonies in winter months (up to 530km) when the Sub-Tropical Front migrates further north of Amsterdam Island (Georges *et al.* 2000a). However, inter-annual and inter-colony differences in the distribution of seals within the different behavioural groups were observed at Îles Kerguelen. This finding implies that our method of diving activity classification may be able to identify temporal and spatial variation in diving activity linked to changes in the marine environment and the distribution of prey. The discriminant function analysis also indicates that this method, at least at Kerguelen, is not only sufficient but also relatively accurate, at differentiating between the diving strategies of seals. The difference observed in proportion of deep versus shallow divers between seals at Cap Noir and Îles Nuageuses in January 2000 indicates that small-scale, localised changes in marine conditions and potentially prey availability affect the diving behaviour of seals.

2.4.3 Conclusions

This study has highlighted the degree of flexibility possible in the diving behaviour of Antarctic fur seals on both an intra- and inter-population level . The differences observed in diving activity between the four groups may reflect differences in prey availability, both in terms of depth and patchiness, as well as the foraging experience and metabolic limits of the individual seals. Whilst the four types of behavioural dive groups have been reported to some extent at other sites, the occurrence of all four together has not previously been noted. The variability in the number of seals using each behavioural dive group between sites and years indicates a shift in dive pattern in response to environmental conditions.

Finally, Bonadonna *et al.* (2001) have recently demonstrated that some Antarctic fur seals return to similar foraging zones in successive foraging trips, suggesting some degree of site fidelity in relation to past experience (Bonadonna *et al.* 2001). A longitudinal examination of the dive behaviour of individuals is necessary to fully interpret the importance of learnt foraging areas to the diving strategies of individual seals.

2.5 SUMMARY

- Intra-population variation in diving behaviour of lactating Antarctic fur seals (*Arctocephalus gazella*) was studied at the Kerguelen Archipelago (49º07'S, 70º45'E) during the austral summers of 1998-2000
- dive data was successfully recorded for 112 seals equipped with time-depth recorders during 117 foraging trips
- all seals displayed bouts of diving activity and the nocturnal foraging behaviour typical of otariids preying on pelagic fish and squid
- mean dive depth (53m) was considerably deeper than recorded for this species at other sites
- four diving behaviour groups were identified: 1. Deep divers (n=60); 2. shallow-active divers (n=45) and 3. shallow divers (n=9) and daytime divers (n=3)
- the distribution of trips assigned to the various behavioural dive groups varied significantly between years
- Antarctic fur seals at Kerguelen exhibit flexible diving strategies both within and between populations.

Chapter 3

Fatty acid composition of lipid-rich myctophids and mackerel icefish - Southern Ocean food-web implications

3.1 Introduction[2]

Myctophids (lanternfish) are the most widespread mesopelagic deep-sea fish family (Saito and Murata 1998), with more than 35 species occurring in the Southern Ocean (Hulley 1998). In addition, many of these species are circumpolar (Hulley 1990), their distribution being determined by the oceanographical structure of Antarctic waters particularly in relation to the Antarctic Circumpolar Current (Sabourenkov 1990). Mesopelagic or pseudoceanic species often exhibit vertical migration from depths of 1000m (Marshall 1971) to 0-200m at night (Hulley 1990; Duhamel *et al.* 2000) in search of prey, where they become accessible to vertebrate, marine predators. In regions of the Southern Ocean where krill, *Euphausia superba,* do not predominate, fish of the family Myctophidae constitute a significant proportion of the diet of Southern Ocean predators (penguins: Adams Klages 1987; Cherel *et al.* 1993; Bost *et al.* 1997; Raclot *et al.* 1998; Hull 1999; seals: Sabourenkov 1991; Daneri and Coria 1993; Reid and Arnould 1996; Cherel *et al.* 1997; Goldsworthy *et al.* 1997; Green *et al.* 1997). The region around the Kerguelen Plateau, in the vicinity of the Kerguelen Archipelago and Heard Island, is one such area. The islands are situated within the Antarctic Polar Frontal Zone, a region of high and seasonal productivity, with zooplankton communities dominated by pelagic crustaceans such as euphausiids and amphipods (Pakhomov and Froneman 2000). Myctophids feeding on meso- and macro-zooplankton including copepods, euphausiids and hyperiid amphipods, migrate vertically to within 50m of the surface at night following the diel migration of the macrozooplankton (Duhamel *et al.* 2000). Guinet *et al.* (1996) estimated that, in 1985, marine predators in the Kerguelen region consumed 460 000 tonnes of myctophids annually. Thus, their role in the ecosystems of the Southern Ocean is substantial.

Some notothenioid fish such as the commercially harvested mackerel icefish, *Champsocephalus gunnari*, also feature in the diet of Antarctic fur seals (Green *et al.* 1991; North 1996; Reid and Arnould 1996; Cherel *et al.* 1997) and King penguins (Moore *et al.* 1998). Given the importance of these fishes to the ecology of many species in the sub-Antarctic, it is surprising that few studies have examined the lipid composition and energy content of myctophids and the mackerel icefish. To date, studies of myctophid lipid composition have centred on North Pacific (Nevenzel *et al.* 1969; Neighbors *et al.* 1988; Moku *et al.* 2000) and sub-Arctic species (Seo *et al.* 1996; Saito and Murata 1998), and in the Antarctic, Phleger *et al.* (1997; 1999) have studied several species from the Scotia Sea and East Antarctica, and Reinhardt and van Vleet (1986) analysed four species from the Antarctic Peninsula. In the southern Indian Ocean, Raclot *et al.* (1998) have recently

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conducted lipid analyses on four species of myctophid occurring in the diet of King Penguins from the Crozet Archipelago in winter and Nichols *et al.* (1994) described the fatty acid (FA) composition of two icefish from the Kerguelen Plateau. Such biochemical studies of prey species are required to complement concurrent studies examining the identification of dietary signature fatty acids in the milk and adipose tissue of marine mammals (Iverson 1993; Grahl-Nielsen and Mjaavatten 1995) and penguins (Raclot *et al.* 1998). In the last decade this technique has evolved as a tool in the identification of prey items to complement conventional methods, which identify hard-parts, such as fish otoliths and squid beaks in faeces. Compositional profiles of the major prey species of myctophid predators, such as Antarctic fur seals, are necessary for comparisons with milk and blubber profiles (Iverson *et al.* 1997a and b; Kirsch *et al.* 2000; Walton *et al.* 2000) and may potentially yield greater knowledge concerning the diet of these predators.

Thus, we describe the lipid composition of Southern Ocean myctophids, particularly in the Kerguelen region, where little information is currently available. Seven species of Myctophidae known to occur in the diet of Antarctic fur seals at Îles Kerguelen (Cherel *et al.* 1997) were analysed: *Gymnoscopelus piabilis, G. nicholsi, G. fraseri, Electrona antarctica, E. subaspera, E. carlsbergi* and *Protomyctophum tenisoni*, in addition to mackerel icefish (*C. gunnari*). We present data for the species studied, which will compliment the FA spectra of prey available to Southern Ocean predators. These data are being incorporated into a study examining the efficacy of using FA signature analysis of fur seal milk samples to identify prey species (see Chapter 4).

Secondly, we examined the geographical variation in lipid composition for three species of myctophid (*E. antarctica, G. fraseri* and *P. tenisoni*) from two sites, the Kerguelen Plateau and Macquarie Ridge, located in the southern Indian and Pacific Oceans respectively. Phleger *et al.* (1997) noted a difference in lipid composition of *E. antarctica* from Elephant Island and East Antarctica, and thus it seems reasonable to assume that geographical variation in fatty acid composition of conspecific fish species may occur in response to regional and seasonal changes in marine productivity and associated changes in zooplankton community structure.

Finally, knowledge of the calorific content of such prey species is necessary for calculating energy flow rates through trophic levels of marine ecosystems (Goldsworthy *et al.* 2001) and in determining the energetic importance of particular prey species in the diet of marine predators (Cherel and Ridoux 1993; Kirkwood and Robertson 1997). Such information is

scarce for many Southern Ocean species, and thus a further aim of this study was to determine the calorific value for each species analysed.

3.2 Materials and methods

3.2.1 Sample collection

Specimens of *P. tenisoni* (n=3), *Electrona subaspera* (n=3), *E. antarctica* (n=2), *E. carlsbergi* (n=2), *Gymnoscopelus piabilis* (n=3), *G. nicholsi* (n=3) and *G. fraseri* (n=3) were collected by RV '*La Curieuse*' during bathypelagic trawls within the preferred foraging zone of female Antarctic fur seals (Guinet *et al.* 2001), to the northeast of the Kerguelen Archipelago (49°07'S, 70°45'E, Fig. 3.1) in June 1998 (Table 3.1). The samples were collected at night using an IYGPT net (International Young Gadoid Pelagic Trawl; opening: 12 x 7 m) with a 10 mm mesh size in the codend (Duhamel *et al.* 2000) and were sorted on deck and frozen. Frozen samples were transported by air to CSIRO Marine Research Laboratories where they remained frozen at –80°C until analysis within two months. The number of fish sampled was limited firstly by the logistical constraints of conducting such studies in the Southern Ocean, and secondly by the difficulties of transporting frozen samples from such remote locations. In addition, analyses of several similar species in previous studies have been performed on comparable sample sizes, with limited variation observed (Phleger *et al.* 1997; 1999; Raclot *et al.* 1998). Whilst comparisons have been made, we recognize the need for further sampling and analyses.

Specimens of *P. tenisoni* (n=3), *G. fraseri* (n=3) and *E. antarctica* (n=2) from Macquarie Ridge (54°35'S, 159°55'E) were included in the study to determine inter-site variation in fatty acid composition. These samples were collected by the CSIRO Marine research vessel '*Southern Surveyor*' from 21-30 January 1999.

Mackerel icefish, *C. gunnari* (n=3), also preyed on by Antarctic fur seals (Cherel *et al.* 1997), were trawled on the southern Kerguelen Plateau at Gunnari Ridge, in the vicinity of Heard Island by MV '*Austral Leader*' during scientific research trawls of the Australian Antarctic Division. Species sampled and the trawl locations (Fig. 3.1) are listed in Table 3.1.

3.2.2 Lipid extraction

Fish were thawed, weighed and a standard length measurement taken. Whole fish, including gut contents, were macerated and the lipid quantitatively extracted overnight by a modified Bligh and Dyer (Bligh and Dyer 1959) one-phase methanol/chloroform/water extraction (1:2:0.8, by volume). The phases were separated the following day by the addition of chloroform, water and sodium chloride (final solvent ratio, 1:1:0.4, by volume,

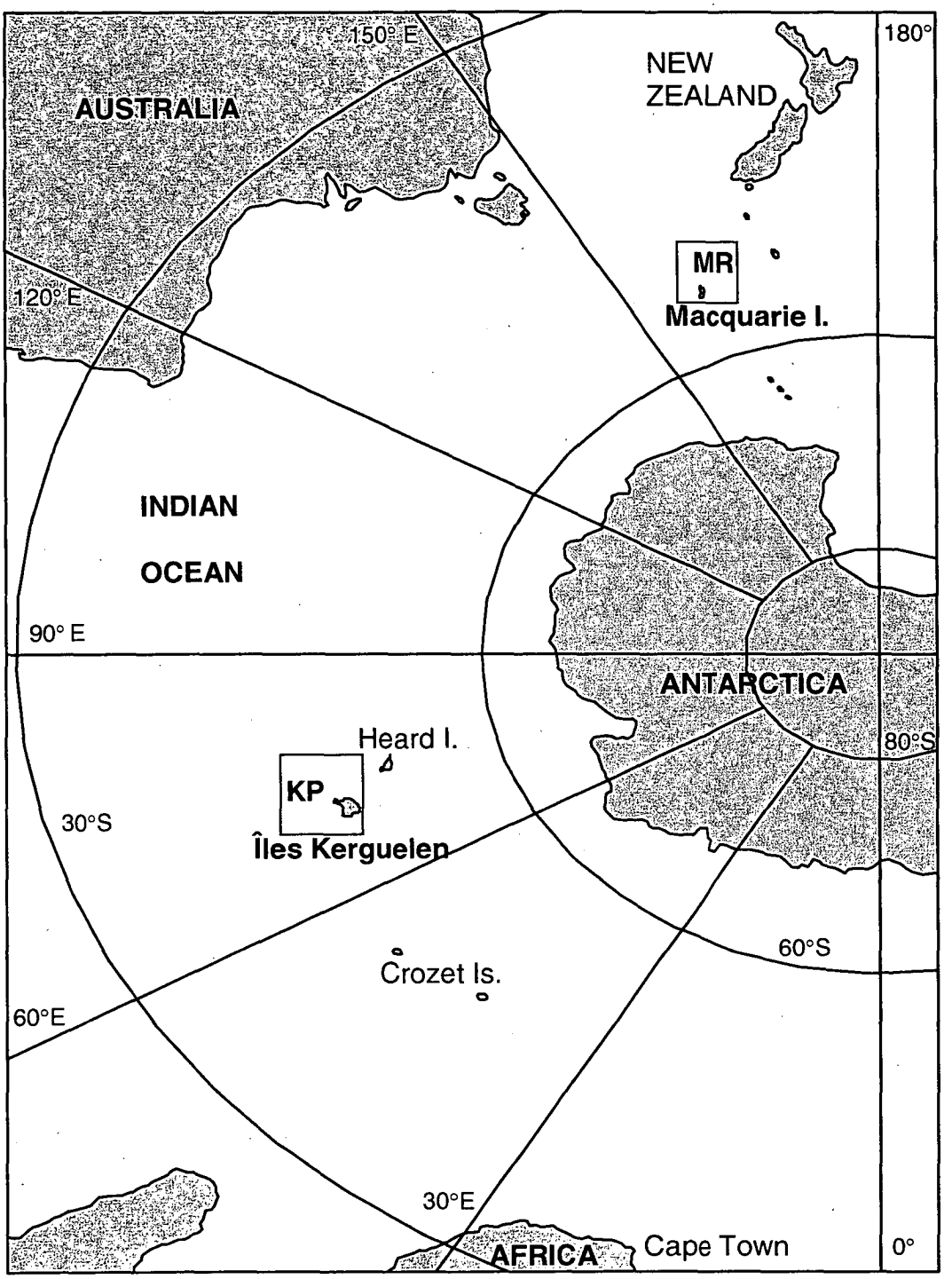

Figure 3.1 A map depicting the sampling regions at the Kerguelen Plateau (KP) and Macquarie Ridge (MR), the Southern Ocean and surrounding subantarctic islands.

Table 3.1: Trawl locations and morphological characteristics of seven species of sub-Antarctic myctophid fish and the channichthyid mackerel icefish.

Species	n	Site	Date	Latitude	Longitude	Standard length (mm)	Mean body mass (g)
Protomyctophum tenisoni	3	KP[a]	14/6/98	49°17'S	71°05'E	40.7 ± 0.6	0.7 ± 0.1
	3	MR[b]	21-30/1/99	54°35'S	159°55'E	49.0 ± 2.0	1.4 ± 0.1
Electrona subaspera	3	KP	14/6/98	49°16'S	71°06'E	72.3 ± 5.0	6.3 ± 1.4
Electrona antarctica	2	KP	14/6/98	49°16'S	71°07'E	82.0± 2.8	7.1 ± 1.6
	3	MR	21-30/1/99	54°35'S	159°55'E	57.7 ± 9.3	2.0 ± 1.0
Electrona carlsbergi	2	KP	14/6/98	49°16'S	71°07'E	89.5 ± 6.4	12.7 ± 5.2
Gymnoscopelus piabilis	3	KP	14/6/98	49°16'S	71°07'E	103.5 ± 10.6[c]	15.3 ± 5.7
Gymnoscopelus nicholsi	3	KP	14/6/98	49°17'S	71°05'E	123.3 ± 5.8	23.5 ± 2.8
Gymnoscopelus fraseri	3	KP	14/6/98	49°16'S	71°07'E	71.7 ± 5.8	4.4 ± 1.4
	3	MR	21-30/1/99	54°35'S	159°55'E	50.7 ± 1.2	1.0 ± 0.1
Champsocephalus gunnari	3	KP	17/3/00	52º35'S	75º11'E	311.7 ± 16.1	131.1± 40.5

[a] KP – Kerguelen Plateau, [b] MR- Macquarie Ridge, [c] standard length available for two of the specimens

methanol/chloroform/water). Concentration of the total solvent extract (TSE) was obtained *in vacuo* by rotary evaporation at 40°C. A sub-sample of the extracted lipid was made up to a known concentration by the addition of chloroform and stored at -20°C. Lipid class analyses were conducted within three days.

An aliquot of the total lipid was analyzed using an Iatroscan MK V TH10 thin-layer chromatography–flame-ionization detector (TLC–FID) analyzer (Tokyo, Japan) to determine the abundance of individual lipid classes (Volkman and Nichols 1991). Samples were applied in duplicate or triplicate to silica gel SIII Chromarods (5μm particle size) using 1μl disposable micropipettes. Chromarods were developed in a glass tank lined with pre-extracted filter paper. The solvent system used for the lipid separation was hexane/diethyl ether/acetic acid (60:17:0.2, by vol), a mobile phase resolving non-polar compounds such as wax esters (WE), triacylglycerols (TAG), free fatty acids (FFA) and sterols (ST). A second non-polar solvent system of hexane/diethyl ether (96:4 vol/vol) was also used for selected samples to separate hydrocarbon from WE and TAG from diacylglyceryl ether (DAGE). After development, the chromarods were oven-dried and analyzed immediately to minimize adsorption of atmospheric contaminants. The FID was calibrated for each compound class [phosphatidylcholine, cholesterol, cholesteryl ester, oleic acid, squalene, wax ester (derived from fish oil), triacyclglycerol (derived from fish oil) and DAGE (purified from shark liver oil); 0.1–10 μg range]. Peaks were quantified on an IBM compatible computer using DAPA software (Kalamunda, Western Australia). Iatroscan results are generally reproducible to ±10% of individual component abundance (Volkman and Nichols 1991).

An aliquot of the total lipid was treated with methanol/hydrochloric acid/chloroform (10:1:1, by volume; 80°C, 2h). After cooling and the addition of MilliQ water (1mL), fatty acid methyl esters (FAME) were extracted into hexane/chloroform (4:1, vol/vol, 3 x 1.5 ml) and the FAME mixture was treated with N,O-bis-(trimethylsilyl)-trifluoroacetamide (BSTFA, 50 μl, 60°C, 1 h) to convert sterols to their corresponding TMSi (trimethylsilyl) ethers.

Gas chromatographic (GC) analyses of FAME were performed with a Hewlett Packard 5890A GC (Avondale, PA) equipped with an HP-5 cross-linked methyl silicone fused silica capillary column (50mx0.32mm i.d.), an FID, a split/splitless injector and an HP 7673A auto sampler. Hydrogen was the carrier gas. Following addition of methyl nonadecanoate and methyl tricosanoate internal standards, samples were injected in splitless mode at an oven temperature of 50°C. After 1 minute, the oven temperature was raised to 150°C at 30°C min^{-1}, then to 250°C at 2°C min^{-1} and finally to 300°C at 5°C min^{-1}. Peaks were quantified with Waters Millenium software (Milford, MA, USA). Individual components were

identified using mass spectral data and by comparing retention time data with those obtained for authentic and laboratory standards. GC results are subject to an error of ±5% of individual component abundance. GC–mass spectrometric (GC–MS) analyses were performed on a Finnigan Thermoquest GCQ system (Austin, TX, USA) fitted with an on-column injector. The GC was fitted with a capillary column similar to that described above.

3.2.3 Calorific content

Whole fish samples of *P. tenisoni*, *E. subaspera*, *E. antarctica*, *E. carlsbergi*, *G. piabilis*, *G. nicholsi*, *G. fraseri* and *C. gunnari* were measured (SL), weighed and oven-dried at 50°C for several days until specimens maintained a constant dry mass. Once dried, the fish were homogenized with a mortar and pestle and either the whole fish or a 0.5g sub-sample was taken. Calorific value (kJ g^{-1} wet and dry mass) of each fish was determined by ballistic bomb calorimetry using a custom-made bomb calorimeter, calibrated by the combustion of pre-weighed benzoic acid thermochemical standard pellets (Vondracek *et al.* 1996).

3.2.4 Statistical analysis

All statistical analyses were conducted using the SYSTAT 9.0 package (SYSTAT Inc., Evanston IL, USA). Means are ± standard deviation unless otherwise stated. A cluster analysis evaluating the similarity of the different fish species was performed using a Bray Curtis dissimilarity matrix on arc-sine transformed (Phillips *et al.* 2001) proportional data of 29 fatty acids (>0.5%). Results are presented graphically by dendrogram. A backwards step-wise discriminant function analysis (DFA) was then used to determine how reliably the fatty acid profiles of the individual fish could be assigned to species cluster groups and which fatty acids were most influential. These analyses were conducted using proportions of the 10 most common fatty acids (14:0, 16:0, 16:1ω7, 18:1ω7, 18:1ω9, 20:1ω9, 20:5ω3, 22:1ω11, 22:6ω3, 24:1ω11) present in the compositional profiles. A jackknife analysis was used to verify the accuracy of the DFA (Tabachnick and Fidel 1996).

3.3 Results

3.3.1 Lipid content and composition

Those species containing notably high concentrations of lipid included *Gymnoscopelus nicholsi* (18% wet mass-WM) and *Electrona antarctica* on the Kerguelen Plateau (KP; 14.3%) and the Macquarie Ridge (MR; 14.5%). *Electrona carlsbergi* (12.2%) and *G. fraseri* (11.6%; Table 3.2).

Two groups were apparent from lipid class profiles. Samples of *E. antarctica* were rich in wax esters (WE, Table 3.2), whilst the remaining myctophid samples and the mackerel

Table 3.2: Lipid composition (% of total lipid) of seven myctophid species and the mackerel icefish, *Champsocephalus gunnari.*

Species	Site	WE	TAG	FFA	ST	PL	Other	Lipid (% WM)
Protomyctophum tenisoni	KP	0.0	59.6±7.4	8.2±1.7	1.1±0.1	27.2±5.9	3.9±1.2	7.8 ± 1.5
	MR	0.1	51.3±14.4	13.1±6.0	5.1±2.6	30.5±5.9	0.0	5.2 ± 1.9
Electrona subaspera	KP	0.0	81.6±6.1	4.1±1.5	1.5±0.2	12.8±4.7	0.0	9.2 ± 1.6
Electrona antarctica	KP	71.6±8.2	17.3±10.3	2.1±0.4	0.6±0.4	7.9±1.7	0.6±0.2	14.3 ± 1.4
	MR	80.2±4.6	2.0±0.2	2.1±0.3	0.6±0.1	14.2±4.7	0.9±0.1	14.5 ± 1.1
Electrona carlsbergi	KP	1.0±0.9	77.8±6.7	3.1±1.5	1.3±0.4	16.5±3.6	0.2±0.3	12.2 ± 3.9
Gymnoscopelus piabilis	KP	0.0	72.7±7.8	9.7±3.3	2.0±1.3	14.7±4.0	1.0±0.8	6.8 ± 1.1
Gymnoscopelus nicholsi	KP	0.0	90.9±0.3	3.4±0.4	0.8±0.1	4.7±0.2	0.2±0.3	18.0 ± 2.3
Gymnoscopelus fraseri	KP	0.2±0.2	78.1±5.4	7.1±1.4	2.2±0.5	12.4±4.0	0.0	11.6 ± 2.9
	MR	0.7±0.2	40.0±7.1	20.4±3.0	8.5±1.1	30.5±3.1	0.0	3.6 ± 0.4
Champsocephalus gunnari	KP	1.0±0.2	45.3±5.9	13.2±1.6	3.0±0.6	37.5±4.5	0.0	3.4 ± 0.4

KP – Kerguelen Plateau, MR- Macquarie Ridge; WE wax ester; TAG triacylglycerol; FFA free fatty acid; ST sterol; PL polar lipid . WM= wet mass.
Other includes DAG -diacylglycerol

icefish, *C. gunnari,* were characterised by high levels (51.3-90.9% of total lipid) of triacylglycerols (TAG), although icefish contained 1.0% WE. *Gymnoscopelus fraseri* from the Macquarie Ridge and icefish were characterized by lower levels of TAG (45.3 and 40.0% WM respectively) and elevated levels of polar lipid, in addition to particularly low percentages of total lipid (approximately 3.5% WM). *Protomyctophum tenisoni* sampled at both sites also contained a relatively high proportion of polar lipid (Table 3.2).

Levels of free fatty acids (FFA) were higher in the Macquarie Island samples of *G. fraseri* (13.1% *cf.* 8.2%) and *P. tenisoni* (20.4% *cf.* 7.1%). We propose that this variability may have resulted from differences either in onboard storage, differences in lipase activity, and/or varying proportions of visceral matter richer in FFA between the samples. Levels of PUFA in several of the species examined in this study were in the range previously determined for these species obtained from other regions (see Raclot *et al.* 1998; Phleger *et al.* 1999), indicating that the protocols used have not degraded individual fatty acids.

3.3.2 Fatty acid profiles

3.3.2.1 TAG-rich species

The eight species analysed were distinguished on the basis of their fatty acid profiles by cluster analysis (Fig. 3.2), identifying three groups: 1) the wax ester-rich myctophid *Electrona antarctica* from the Kerguelen Plateau and Macquarie Ridge; 2) other myctophid species and 3) the ice fish *C. gunnari*. Icefish differed considerably in fatty acid composition from that of the myctophid species, containing high levels of palmitoleic acid (16:1ω7) and eicosapentaenoic acid (EPA, 20:5ω3) in comparison to other species and a generally greater proportion of polyunsaturated fatty acids (PUFA; Fig. 3.3 and Table 3.3) than other myctophids collected at the Kerguelen Plateau. The two TAG-rich species sampled at Macquarie Ridge, *G. fraseri* and *P. tenisoni*, were clustered together (Fig. 3.2).

Within the myctophid group, individual species were generally well separated on the basis of their fatty acid signatures (Fig. 3.2). All species of Myctophidae studied contained relatively high levels of monounsaturated fatty acids (MUFA; 33.8-53.5% of total FA). Of the two TAG-rich *Electrona* congeners, *E. carlsbergi* contained higher relative levels of 14:0, 16:1ω7, oleic acid (18:1ω9), 20:1ω9 and 20:5ω3 than *E. subaspera* (Table 3.3). The long-chain MUFA 22:1ω11, 22:1ω9, 24:1ω11, and 18:4ω3 were more prevalent in *E. subaspera. Protomyctophum tenisoni* from the Kerguelen Plateau was separated from the Macquarie Ridge specimens, and grouped with fish from the genus *Gymnoscopelus*. MR *P. tenisoni* contained a higher proportion of the essential PUFA decosahexaenoic acid (DHA, 22:6ω3), and lower relative levels of several MUFA: 16:1ω7, 22:1ω11 and 24:1ω11.

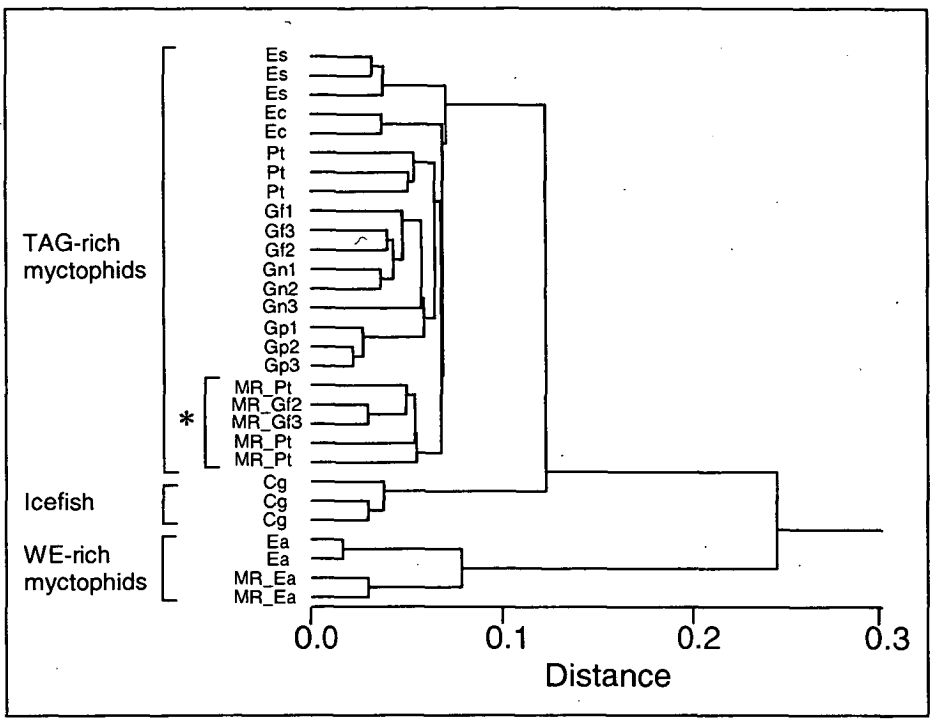

Figure 3.2 A dendrogram based on a Bray-Curtis dissimilarity matrix for seven species of myctophids and the mackerel icefish, *Champsocephalus gunnari* (Cg) from the Kerguelen Plateau and Macquarie Ridge (MR). *highlights TAG-rich specimens from Macquarie Ridge.

Ea – *Electrona antarctica*, Ec – *E. carlsbergi*, Es – *E. subaspera*, Gf – *Gymnoscopelus fraseri*, Gn – *G. nicholsi*, Gp – *G. piabilis*, Pt – *Protomyctophum tenisoni.*

Table 3.3: Fatty acid composition (% of total lipid) of seven myctophids *P. tenisoni* (KP and MR), *E. subaspera* (KP), *E. carlsbergi* (KP), *G. piabilis* (KP), *G. nicholsi* (KP), *G. fraseri* (KP and MR) and the icefish *C. gunnari* (KP). Values ± SD.

Fatty acids	*Protomyctophum tenisoni* KP (n=3)	*Protomyctophum tenisoni* MR (n=3)	*Electrona subaspera* KP (n=3)	*E. carlsbergi* KP (n=2)	*Gymnoscopelus piabilis* KP (n=3)	*G. nicholsi* KP (n=3)	*G. fraseri* KP (n=3)	*G. fraseri* MR (n=3)	*Champsocephalus gunnari* KP (n=3)
14:0	5.4 ± 1.2	2.7 ± 0.5	2.7 ± 0.2	4.9 ± 0.4	4.8 ± 0.2	5.5 ± 0.3	5.6 ± 0.2	3.3 ± 0.3	5.8 ± 1.0
15:0	0.7 ± 0.1	0.5 ± 0.1	0.5 ± 0.0	0.3 ± 0.1	0.6 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.3 ± 0.0
16:0	20.0 ± 0.7	17.4 ± 0.5	17.1 ± 0.6	17.8 ± 1.2	19.2 ± 0.6	14.5 ± 0.6	15.8 ± 0.9	17.5 ± 1.2	19.8 ± 0.5
18:0	2.5 ± 0.4	3.1 ± 0.3	3.1 ± 0.4	3.1 ± 0.3	4.1 ± 0.1	3.8 ± 0.3	3.0 ± 0.3	3.3 ± 0.2	1.5 ± 0.3
20:0	0.3 ± 0.0	0.2 ± 0.0	0.5 ± 0.1	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.0	0.03 ± 0.0
Total SFA	28.9 ± 2.4	23.9 ± 1.4	23.9 ± 1.3	26.3 ± 2.0	28.9 ± 1.0	24.3 ± 1.4	25.1 ± 1.6	24.7 ± 1.8	27.4 ± 1.8
16:1ω7	6.5 ± 1.0	4.5 ± 0.8	5.4 ± 0.5	8.6 ± 0.1	5.8 ± 0.6	5.3 ± 0.4	5.6 ± 0.8	3.6 ± 0.1	11.5 ± 0.7
16:1ω7t*	0.3 ± 0.2	0.1 ± 0.2	0.6 ± 0.1	0.3 ± 0.5	0.6 ± 0.1	0.5 ± 0.1	0.4 ± 0.3	0.5 ± 0.0	1.0 ± 0.1
18:1ω9	14.8 ± 0.6	14.0 ± 1.0	15.0 ± 3.2	17.8 ± 0.4	18.6 ± 1.3	16.6 ± 3.4	13.7 ± 0.8	13.3 ± 0.4	13.5 ± 1.0
18:1ω7	3.3 ± 0.7	4.4 ± 0.3	2.8 ± 0.3	3.2 ± 0.2	5.3 ± 0.4	8.2 ± 0.6	5.9 ± 1.4	4.3 ± 0.3	5.4 ± 0.2
18:1ω5	0.9 ± 0.1	0.7 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.7 ± 0.0	0.9 ± 0.0	0.6 ± 0.0	0.3 ± 0.0
20:1ω9	3.9 ± 1.4	7.7 ± 2.4	1.8 ± 0.4	4.3 ± 1.3	7.3 ± 0.7	14.5 ± 0.7	9.1 ± 0.9	7.2 ± 1.9	2.5 ± 0.4
20:1ω7	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.0	0.5 ± 0.2	0.6 ± 0.0	0.7 ± 0.1	0.6 ± 0.1	0.4 ± 0.0	0.3 ± 0.0
22:1ω11	4.1 ± 0.4	2.3 ± 0.5	8.5 ± 1.3	4.2 ± 0.2	1.9 ± 0.2	3.3 ± 1.8	4.9 ± 1.1	1.1 ± 0.3	0.2 ± 0.2
22:1ω9	2.1 ± 0.2	1.2 ± 0.2	3.7 ± 0.5	2.2 ± 0.1	1.1 ± 0.0	1.6 ± 0.6	2.2 ± 0.4	0.7 ± 0.1	0.4 ± 0.1
24:1ω11	2.3 ± 0.2	0.9 ± 0.3	4.0 ± 0.6	1.4 ± 0.1	0.7 ± 0.2	1.1 ± 0.8	1.5 ± 0.5	0.4 ± 0.1	0.1 ± 0.2
24:1ω9	1.7 ± 0.1	1.3 ± 0.3	1.5 ± 0.1	1.4 ± 0.2	1.1 ± 0.2	1.0 ± 0.4	1.6 ± 0.2	1.7 ± 0.2	0.4 ± 0.1
Total MUFA	40.3 ± 5.0	37.4 ± 6.2	44.6 ± 7.1	44.7 ± 3.4	43.7 ± 3.8	53.5 ± 7.9	46.4 ± 6.5	33.8 ± 3.4	35.6 ± 3.0
18:2ω6	1.4 ± 0.1	1.3 ± 0.3	1.7 ± 0.0	1.4 ± 0.1	1.7 ± 0.1	1.7 ± 0.5	1.5 ± 0.1	1.4 ± 0.1	1.8 ± 0.4
18:4ω3	1.7 ± 0.3	1.2 ± 0.3	2.3 ± 0.4	1.3 ± 0.0	1.3 ± 0.1	1.0 ± 0.1	1.6 ± 0.2	1.3 ± 0.1	1.1 ± 0.1
20:4ω6	0.5 ± 0.0	0.7 ± 0.1	0.5 ± 0.1	0.8 ± 0.0	0.6 ± 0.1	0.4 ± 0.1	0.5 ± 0.0	0.9 ± 0.0	0.9 ± 0.2
20:5ω3	7.9 ± 0.5	9.6 ± 1.1	8.5 ± 0.5	10.2 ± 0.5	7.0 ± 0.4	6.7 ± 1.1	8.6 ± 0.4	9.8 ± 0.5	16.5 ± 0.2
20:4ω3	0.5 ± 0.4	0.8 ± 0.1	1.2 ± 0.1	0.5 ± 0.0	1.2 ± 0.2	0.8 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	0.4 ± 0.0
20:2ω6	0.4 ± 0.3	0.1 ± 0.1	0.6 ± 0.0	0.2 ± 0.0	0.5 ± 0.1	0.4 ± 0.1	0.2 ± 0.2	0.4 ± 0.1	0.3 ± 0.1
22:6ω3	12.2 ± 0.1	18.9 ± 2.9	11.0 ± 1.1	9.4 ± 0.3	8.3 ± 1.8	5.5 ± 0.2	8.8 ± 1.2	20.5 ± 0.1	10.7 ± 0.5
22:5ω3	0.7 ± 0.0	1.4 ± 0.8	1.0 ± 0.1	0.7 ± 0.1	1.1 ± 0.0	1.0 ± 0.2	1.1 ± 0.1	1.2 ±0.1	0.6 ± 0.0
Total PUFA	25.3 ± 1.7	34.0 ± 5.7	26.8 ± 2.3	24.5 ± 1.0	21.7 ± 2.8	17.5 ± 2.4	23.4 ± 2.3	36.6 ± 1.1	32.2 ± 1.5
Other	5.5 ± 1.5	4.7 ± 1.0	4.7 ± 1.2	4.5 ± 0.7	5.7 ± 0.8	4.7 ± 1.6	5.1 ± 0.7	4.9 ± 0.4	4.8 ± 1.2
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Total (ω3FA)	21.6	30.5	22.0	20.6	18.0	13.9	19.5	32.6	29.2
Total (ω6FA)	2.4	2.3	2.9	2.6	3.0	2.7	2.4	2.8	3.4
Ratio ω3/ω6	9.0	13.3	7.6	7.9	6.0	5.1	8.1	11.6	8.6

Other <0.5%: 14:1ω5, 4,8,12TMTD, iso15:0, a15:0, C_{16}PUFA, iso16:0, 16:1ω9, 16:1ω5, br17:1, i17:0, a17:0, 17:1ω8, 17:1ω6, 17:1, 17:0, 18:1ω7t, 18:1, 19:1, 18:3ω6, 20:3ω6, C_{20}PUFA, 20:1ω5, C_{21}PUFA, 22:5ω6, 22:1ω7, 22:0, 24:0; *16:2 celutes with 16:1ω7t.

Gymnoscopelus nicholsi, the largest and most lipid-rich of the *Gymnoscopelus* species studied, contained the highest levels of MUFA (53.5%) of all species analysed and accordingly, the lowest proportion of PUFA (17.5%; Fig. 3.3). Levels of 20:1ω9 and 18:1ω7 were particularly elevated, whilst the proportion of 22:6ω3 was low in comparison to that of other myctophids (Table 3.3). *Gymnoscopelus fraseri* appeared to be more similar to *G. nicholsi* (Fig. 3.2), containing high levels of MUFA (46.4%), although the PUFA 20:5ω3 and 22:6ω3 were present in higher proportions. *Gymnoscopelus piabilis*, also one of the larger myctophids, differed from the other two species of *Gymnoscopelus*, containing higher levels of saturated fatty acids (SFA), particularly 16:0 (Table 3.3). Proportions of 18:1ω9 (18.6%) were also the highest recorded in any of the fishes sampled (Table 3.3). Fish were generally high in ω3 fatty acids in comparison to ω6 fatty acids. TAG-rich specimens from MR showed the highest ω3/ω6 ratio (11.6 and 13.3) with values of 5.1 to 9.0 observed for KP TAG-rich myctophids (Table 3.3).

3.3.2.2 Wax ester-rich species

Electrona antarctica specimens contained high levels of MUFA (65.4% and 67.5%) in comparison to other species (Tables 3.3 and 3.4). The fatty acid profile of *E. antarctica* was characterised by particularly high proportions of 18:1ω9 (32 - 34%), followed by 16:1ω7, 22:6ω3, 20:5ω3 and 16:0. Saturated fatty acids comprised only 9.1 and 11.1% of the total fatty acids for *E. antarctica* from KP and MR respectively, values which are low in comparison to those of the TAG-rich species.

Overall, saturated and mono-unsaturated fatty alcohols occurred in similar proportions in *E. antarctica* collected from the two regions. However, a number of differences in the relative proportions of individual components were apparent. *Electrona antarctica* from the Kerguelen Plateau were highest in 16:0, 18:1ω9 and 16:1ω9 fatty alcohols (Table 3.4). Samples from Macquarie Ridge showed a similar profile, although 20:1ω9 was the major fatty alcohol present, and 14:0 and 18:1ω7 were also elevated. The ω3/ω6 FA ratio was similar between sites although absolute percentages of ω3 and ω6 fatty acids differed (Table 3.4).

Six fatty acids (16:0, 18:1ω9, 20:1ω9, 22:1ω11, 20:5ω3, 22:6ω3) were identified by a backwards-stepwise DFA (see Methods) as distinguishing the fatty acid profiles of the ten species cluster groups (Wilks' $Lambda_{6,9,19}$= 0.0000; $F_{54,75}$=47.115, P<0.001). A jackknife classification matrix reassigned individual profiles to the species cluster groups in 97% of cases indicating that these six fatty acids were strong predictors of the species cluster groups (Fig. 3.4).

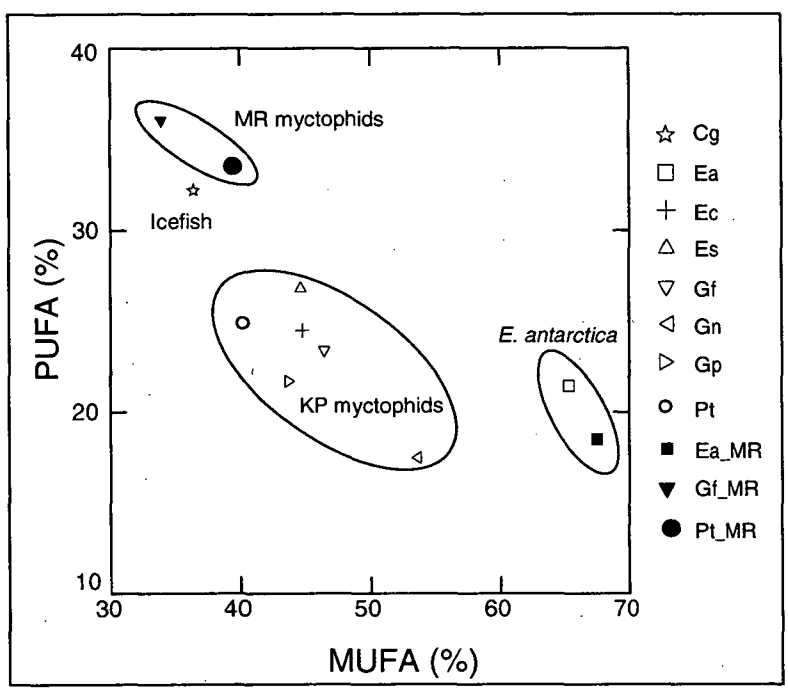

Figure 3.3 A plot of the proportion of monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA) present in myctophids and the mackerel icefish from the Kerguelen Plateau and the Macquarie Ridge (MR). Legend as for Figure 3.2.

3.3.3 Geographic variation in fatty acid composition

The fatty acid profiles of TAG-rich *P. tenisoni* and *G. fraseri* from Macquarie Ridge were more similar to each other than to conspecifics from the Kerguelen Plateau (Fig. 3.2) and contained higher levels of PUFA (Fig. 3.3). Interestingly, *G. fraseri* from Macquarie Ridge had much lower lipid levels (3.6%) than those from the Kerguelen Plateau (11.6%, Table 3.2), which may have been due to the disparity in size of specimens from the two sites. *G. fraseri* specimens from Macquarie Ridge were smaller in length and mass (Table 3.1). Both species also contained considerably higher levels of 22:6ω3 and 20:5ω3 fatty acids at the Macquarie Ridge than on the Kerguelen Plateau (Table 3.3).

Table 3.4: Fatty acid and fatty alcohol composition of *Electrona antarctica* from the Kerguelen Plateau and Macquarie Ridge.

	Alcohols		Fatty Acids	
	KP	MR	KP	MR
14:0	7.9 ± 0.5	10.8 ± 0.2	1.7 ± 0.2	2.7 ± 0.1
15:0	0.8 ± 0.1	0.6 ± 0.0	0.1 ± 0.1	0.1 ± 0.0
16:0	37.0 ± 1.7	33.9 ± 1.6	5.3 ± 0.3	6.7 ± 0.1
18:0	2.2 ± 0.1	1.9 ± 0.3	2.0 ± 0.2	1.6 ± 0.0
Total SFA	47.7 ± 2.4	47.2 ± 2.1	9.1 ± 0.8	11.1 ± 0.2
16:1ω9	5.7 ± 0.6	4.9 ± 0.1	0.3 ± 0.0	0.3 ± 0.0
16:1ω7	0.9 ± 0.1	0.9 ± 0.1	17.2 ± 0.9	16.2 ± 0.1
16:1ω5	0.8 ± 0.1	0.9 ± 0.0	0.3 ± 0.0	0.3 ± 0.0
18:1ω9	27.3 ± 1.8	19.8 ± 2.4	34.4 ± 0.8	32.1 ± 1.5
18:1ω7	5.3 ± 0.2	6.8 ± 0.6	3.9 ± 0.3	5.8 ± 0.4
18:1ω5	1.2 ± 0.1	1.3 ± 0.1	0.6 ± 0.0	0.2 ± 0.0
20:1ω9	3.4 ± 0.1	10.5 ± 2.6	2.9 ± 0.5	7.4 ± 0.7
20:1ω7	0.4 ± 0.0	0.4 ± 0.0	0.7 ± 0.0	0.7 ± 0.0
22:1ω11	0.8 ± 0.0	1.6 ± 0.1	2.0 ± 0.4	2.0 ± 0.2
22:1ω9	0.9 ± 0.2	0.9 ± 0.2	1.5 ± 0.2	1.3 ± 0.1
24:1ω7	0.4 ± 0.0	0.5 ± 0.3	1.7 ± 0.4	1.2 ± 0.2
Total MUFA	47.1 ± 3.2	48.5 ± 6.5	65.4 ± 3.5	67.5 ± 3.2
18:4ω3	0.0	0.0	2.0 ± 0.1	1.6 ± 0.0
18:2ω6	0.0	0.0	1.5 ± 0.0	1.4 ± 0.1
20:4ω6	0.0	0.0	0.7 ± 0.0	0.5 ± 0.0
20:5ω3	0.0	0.0	6.0 ± 0.0	6.8 ± 0.1
20:4ω3	0.0	0.0	0.6 ± 0.0	0.4 ± 0.0
22:6ω3	0.0	0.0	10.0 ± 0.1	7.3 ± 0.2
22:5ω3	0.0	0.0	0.6 ± 0.0	0.5 ± 0.0
Total PUFA	0.0	0.0	21.4 ± 0.2	18.5 ± 0.4
Other	5.2 ± 0.4	4.3 ± 0.4	4.1± 0.6	2.9 ± 0.4
Total	100.0	100.0	100.0	100.0
Total ω3 FA	.	.	19.2	16.6
Total ω6 FA	.	.	2.2	1.9
Ratio ω3/ω6	.	.	0.11	0.11

Other <0.5%: 14:1ω5, a15:0, iso15:0, C_{16}PUFA, 17:0, a17:0, iso17:0, 17:1, 18:1, 18:3ω6, 20:0, 20:1ω5, 20:1ω11, 20:2ω6, 20:3ω6, 22:5ω6, 22:0, 22:1ω7, 4,8,12TMTD.
SFA= saturated fatty acids; MUFA=monounsaturated fatty acids; PUFA= polyunsaturated fatty acids.

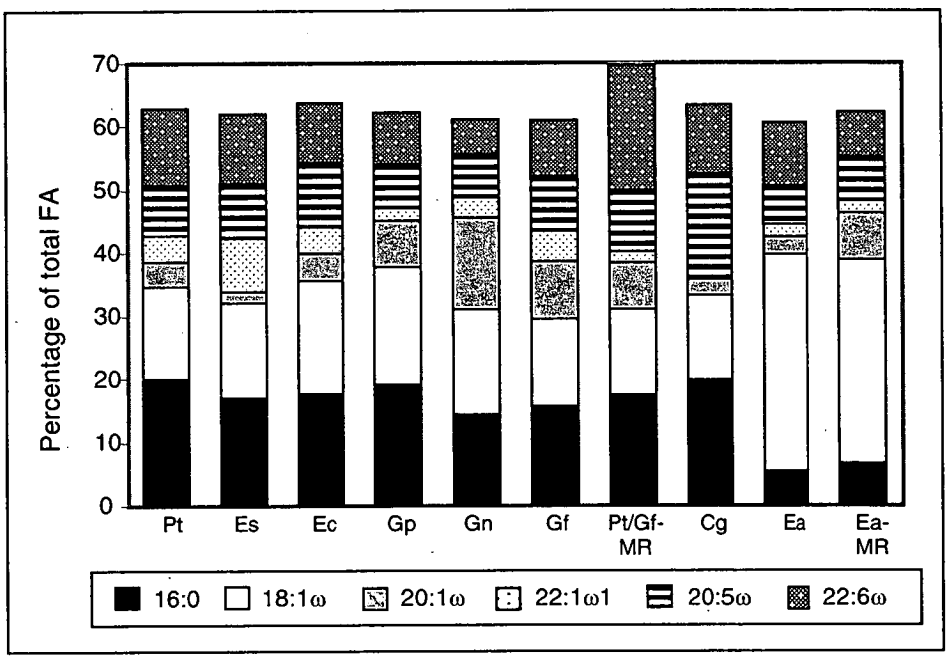

Figure 3.4 Relative proportions of the six most common fatty acids found in the ten species cluster groups identified by MDS. Legend as for Figure 3.2. MR-Macquarie Ridge

The fatty acid and fatty alcohol composition of *E. antarctica* from the two sites differed in that specimens from the Macquarie Ridge had higher proportions of 20:1ω9, 18:1ω7 and 14:0 fatty acids and fatty alcohols, while those from the Kerguelen Plateau contained higher levels of 16:0 and 18:1ω9 fatty alcohols (Table 3.4).

3.3.4 Water and calorific content

The water content of the eight species of fish varied considerably, ranging from 60.8 to 76.7% of wet mass. The wax ester-rich *Electrona antarctica* contained the least water in addition to the highest calorific value of 34.3 kJ per gram of dry mass (Table 3.5). This value is in accordance with the high lipid content (14.3%) reported earlier for *E. antarctica* (Table 3.1). The relationship between percentage water content and mean energy content (kJ g^{-1} WM) was highly, negatively significant (Fig. 3.5; $P<0.001$, n=8, $r^2=0.902$). A positive relationship between size and calorific content was present for some species such as *G. piabilis and E. carlsbergi*, whilst for other species there was no trend, although sample size was limited.

Table 3.5: Calorific content of seven species of myctophid fish and the mackerel icefish, *Champsocephalus gunnari*, from the Îles Kerguelen region.

Species	n	Standard length (mm)	Wet mass (g)	Water content (%)	kJ g^{-1} dry mass	kJ g^{-1} wet mass
Protomyctophum tenisoni	1	45	0.9	74.6	24.2	6.1
Electrona subaspera	3	92.7±7.5	11.8±4.3	72.3±1.6	26.6±2.1	7.4±1.0
Electrona antarctica	5	64.5±8.6	3.2±1.8	60.8±8.8	34.3±3.8	13.3±2.6
Electrona carlsbergi	6	84.7±3.6	8.7±2.2	67.0±3.2	25.9±3.2	8.6±1.2
Gymnoscopelus piabilis	5	187.6±32.0	74.6±30.7	68.5±3.0	30.0±2.6	9.5±1.7
Gymnoscopelus nicholsi	1	128	22.0	66.8	28.0	9.8
Gymnoscopelus fraseri	5	66.2±7.1	3.0±1.7	62.6±10.1	27.0±2.9	10.2±3.5
Champsocephalus gunnari	3	311.7±16.1	130.1±40.5	76.7±2.0	23.2±0.6	5.4±0.3

Calorific content per gram wet mass ranged between 5.4 kJ g^{-1} and 13.3 kJ.g^{-1} for *C. gunnari* and *E. antarctica* respectively. Calorific values per gram dry mass were also variable (23.2-34.3 kJ) as a result of the variability in water content for the various species. The mean calorific value for myctophids from the Kerguelen Plateau was high at 9.3 kJ g^{-1} WM.

3.4 Discussion

3.4.1 Total lipid, lipid classes and calorific value

Myctophids from the Kerguelen Plateau examined in this study were generally rich in lipid levels (7.8-18.0% WM) whilst the mackerel icefish was relatively lipid-poor (3.4% WM). *Gymnoscopelus nicholsi* and *Electrona antarctica* were particularly oily fishes, comprised of 18.0% and 14.5% WM respectively. Species examined from the Macquarie Ridge area were

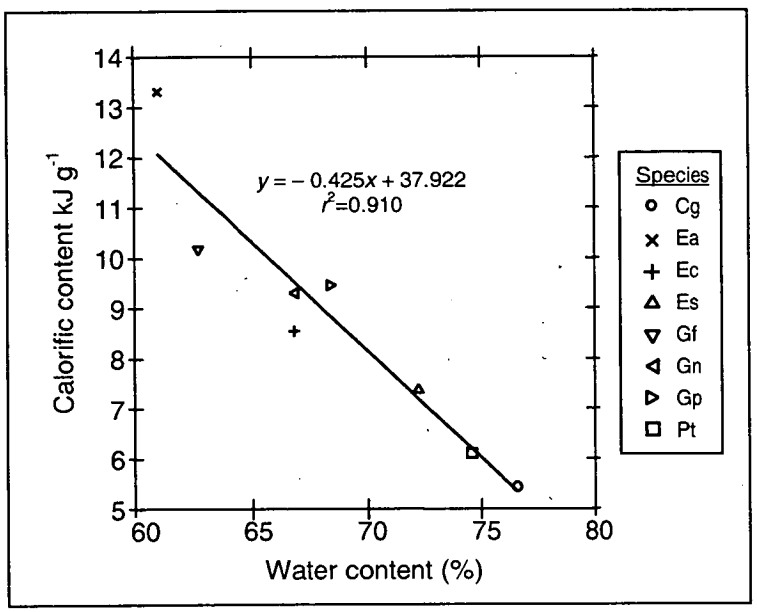

Figure 3.5 A regression of water and energy content (kJ g^{-1} wet mass) of 7 species of myctophid and mackerel icefish from the Kerguelen Plateau. Legend as for Figure 3.2.

generally lower in lipid content, excepting *E. antarctica*, which exhibits some of the highest lipid levels for any species of fish regardless of location (East Antarctica: Reinhardt and van Vleet 1986; Phleger *et al.* 1997; Kerguelen Plateau and Macquarie Ridge: this study). Values are comparable to those reported by Seo *et al.* (1996) and Saito and Murata (1998) for myctophids of the sub-Arctic (6.7-21.7% and 4.4-26.1% WM respectively).

Reinhardt and van Vleet (1986) noted that percentage lipid increased with depth in many Antarctic fish species. It appears that this may not necessarily be the case for myctophid species in waters surrounding the Kerguelen Archipelago. The more lipid-rich species such as *G. nicholsi, G. fraseri, E. antarctica* and *E. carlsbergi* were all present in 300m trawls during the day, whilst *E. subaspera* and *G. piabilis* (9.2 and 6.8% lipid respectively) were only detected during night trawls, indicating they inhabit depths in excess of 300m during the day (Duhamel *et al.* 2000). Further targeted sampling and lipid analyses are necessary to examine such a trend.

TAG was the primary lipid class in all species except *E. antarctica,* which was rich in WE (71.6-80.2% of total lipid). Specimens of *E. antarctica* from Elephant Island, the Antarctic Peninsula and East Antarctica were also found to be high in WE, which is thought to play a role in buoyancy and long term energy storage (Reinhardt and van Vleet 1986; Phleger *et al.* 1997, 1999). Myctophids characterised by high levels of WE in the sub-Arctic generally tend to be stationary species, inhabiting deep water, and not undergoing the diurnal vertical migration typical of many other myctophids (Seo *et al.* 1996). Our findings of WE-rich *E. antarctica* in surface waters of the Polar Frontal Zone (KP) and at Macquarie Ridge support the observations of Phleger *et al.* (1999) that both TAG and WE-rich species are successful in all regions of the Antarctic Ocean.

In terms of calorific value, myctophids exhibit some of the highest values for any fish species. In this study, values ranged from 6.1-13.3 kJ g^{-1}WM, for species from the Kerguelen Plateau. Tierney *et al.* (2002) reported similar values for Southern Ocean myctophids from the Macquarie Ridge (5.4-10.9 kJ g^{-1}) as have Cherel and Ridoux (1992), who recorded values of 7.0 and 8.1 kJ g^{-1} for *E. carlsbergi* and *Krefftichthys anderssoni* respectively from the Crozet Archipelago. *Champsocephalus gunnari*, however, was relatively low in energy content (5.4 kJ g^{-1}WM) and more comparable to the calorific content of the majority of fish species eaten by Cape fur seals, *Arctocephalus pusillus pusillus*, in South Africa (3.7-7.7 kJ g^{-1}) as studied by Balmelli and Wickens (1994). Squid, also a preferred food item of many Southern Ocean marine predators (Slip 1995; Rodhouse *et al.* 1996; Cherel and Weimerskirch 1999) are remarkably low in energy content when compared to the lipid-rich

Myctophidae with the majority of species ranging from 2.0-4.0 kJ g^{-1}WM (Croxall and Prince 1982).

3.4.2 Fatty acid and alcohol composition

MUFA comprised the majority of FA of all myctophids (40.3-65.4%) from the Kerguelen Plateau, as was reported by Saito and Murata (1998) for 13 sub-Arctic species, who suggested that high monoene content be considered characteristic of this family. However, the two TAG-rich species from the Macquarie Ridge, *Gymnoscopelus fraseri* and *Protomyctophum tenisoni*, contained similar levels of MUFA and PUFA (33.8-37.4%), perhaps indicating differing dietary intake between the two regions. The levels of MUFA present in mackerel icefish more closely approximated those of myctophids from Macquarie Ridge than any species sampled from the Kerguelen Plateau, and were two-fold higher than levels reported for specimens from Heard Island further south on the Kerguelen Plateau (Nichols *et al.* 1994).

All fish contained relatively high levels of 16:0, 18:1ω9, 22:6ω3, 20:5ω3 and 20:1ω9 fatty acids. *G. nicholsi* contained notably higher levels of 20:1ω9 fatty acid than other species (14.5% *cf* 1.8-9.1%). Raclot *et al.* (1998) found *G. piabilis* from the Crozet Archipelago to be rich in 20:1ω9, whereas in 1998 on the Kerguelen Plateau, *G. piabilis* was particularly high in 16:0 and 18:1ω9. Raclot *et al.* (1998) also reported that the major fatty acids in the four species of myctophid they studied (*G. piabilis, Lampichthys procerus, Metelectrona ventralis* and *P. bolini*), were consistently 18:1ω9, 16:0, 22:6ω3 and 20:1ω9.

The fatty acid composition of the nocturnally bentho-pelagic icefish differed to that of the myctophids, being high in 16:0, 16:1ω7, 20:5ω3 and 22:6ω3 fatty acids. The diet of *C. gunnari* at Kerguelen consists primarily of the crustacean, *Euphausia vallentini,* the hyperiid amphipod, *Themisto gaudichaudii,* and occasional fish (Duhamel 1987). The small proportion of WE (1.0%) recorded in the lipid composition of *C. gunnari* may represent the consumption of occasional *E. antarctica* or *G. braueri,* also high in WE (Phleger *et al.* 1999). *T. gaudichaudii* comprises an important local component of the macrozooplankton community where it is the main prey for many planktivorous seabirds inhabiting the Kerguelen Archipelago (Bocher *et al.* 2001). Nelson *et al.* (2001) reported high levels of 16:0, 20:5ω3 and 22:6ω3 fatty acids (51.7% of total fatty acids) in *T. gaudichaudii* from the Elephant Island region, Antarctica, as did Phleger *et al.* (1998). The presence of the diatom trophic marker fatty acid 16:1ω7, as found in *C. gunnari*, is usually indicative of phytoplankton ingestion in zooplankton communities (Hagen *et al.* 2001). The cnidarian, *Calycopsis borchgrevinki,* and the chaetognath, *Sagitta gazellae,* both displayed high levels of 16:1ω7 in comparison to other zooplankton studied (Phleger *et al.* 1998). A recent study

by Gurney *et al.* (2001) of the trophic position of euphausiids in the vicinity of the sub-Antarctic Prince Edward Islands indicates that juveniles of *E. vallentini* are in fact herbivorous, which may explain the higher proportion of diatom-derived lipids found in *C. gunnari* relative to other fishes analysed.

3.4.3 Trophic relationships and spatial variation in fatty acid composition

Myctophids primarily consume herbivorous zooplankton (Kozlov and Tarverdiyeva 1989), which include copepods, euphusiids and hyperiid amphipods. The diet may also be dependent upon intra-species variation in fish size, for example, smaller individuals of *E. antarctica* may subsist of a diet primarily composed of copepods and hyperiid amphipods while larger fish are capable of consuming euphausiids (Kozlov and Tarverdiyeva 1989).

It is clear from the results of this study that species of Myctophidae, while similar in general lipid composition may be distinguished from each other on the basis of fatty acid composition. Variations observed represent real inter-species differences arising from dietary differences and based on the use of common methodologies, are we believe, not artifacts due to sampling or analytical techniques. Saito and Murata (1998) in their study of the FA spectra of sub-Arctic myctophids and their prey, noted a relationship between the high monoene levels of myctophid stomach contents and their tissues, suggesting that prey lipids may be incorporated into tissue FA with little modification. Several species from the Kerguelen Plateau (*E. subaspera, G. nicholsi and G. fraseri*) contained particularly high levels of the fatty acids 20:1ω9 and 22:1ω11, which are indicative of a diet containing copepods (Dahl *et al.* 2000).

Specimens of a species collected from different sites may also vary significantly in their fatty acid composition as was the case in this study where *Protomyctophum tenisoni* and *Gymnoscopelus fraseri* from the Kerguelen Plateau contained higher levels of lipid and different proportions of major fatty acids than conspecifics trawled on the Macquarie Ridge. These differences may relate to variability in food availability between the sites (Fig. 3.2, Phleger *et al.* 1997) and/or to the age, size and condition of fish, as has been demonstrated by Wilson and Nichols (2001) for Patagonian toothfish, *Dissostichus eleginoides.* Proportions of 16:0, 16:1ω7, 22:1ω9 and 22:1ω11 FA (and 20:1ω9 in *G. fraseri*) were also higher in specimens inhabiting waters east of the Kerguelen Archipelago, while fish from the Macquarie Ridge contained higher levels of 20:5ω3 (EPA) and 22:6ω3 (DHA) which are known to be typical of crustaceans such as hyperiid amphipods, and polychaetes (Phleger *et al.* 1998, 2000; Nelson *et al.* 2001). EPA and DHA are useful as biomarkers as they cannot be synthesized by marine zooplankton and must be obtained from the diet (Phleger *et al.* 2000). A recent study of the diet composition and guild structure of myctophids at

Macquarie Island has found *Electrona antarctica* and *P. teninsoni* to be copepod feeders, while *G. fraseri*, *G. piabilis* and *G. nicholsi* are more generalist feeders, preying on euphausiids, copepods and hyperiid amphipods (Gaskett *et al.* 2001). Thus, differences in fatty acid composition of the myctophids studied may be attributable to the differential consumption between sites of the various species of herbivorous zooplankton, and any variation in phytoplankton species consumed by them.

Interestingly, the fatty acid and fatty alcohol profiles of *E. antarctica,* from Kerguelen and the Macquarie Ridge while appearing similar overall, differed in levels of 20:1ω9 fatty acid and alcohol which were higher at the Macquarie Ridge. Phillips *et al.* (2001) have also noted 20:1ω9, along with 18:1ω9, as being the major fatty acids found in the squid *Moroteuthis ingens* at Heard and Macquarie Islands, and have highlighted the existence of a copepod-myctophid-*M.ingens*-higher predator food chain. A similar food-chain had previously been proposed for the ommastrephid squid, *Martialia hyadesi*, at South Georgia by Rodhouse *et al.* (1992). It would seem that copepods constitute an important dietary component of all three species sampled from Macquarie Ridge. *Electrona antarctica* is also known to be an important predator of krill (Greely *et al.* 1999) which are high in 18:1ω9 (Hagen *et al.* 2001). The notably high levels of 18:1ω9 found in specimens of *E. antarctica* from both the Kerguelen Plateau and Macquarie Ridge also confirm this trophic link.

Levels of 18:1ω9 fatty alcohol, were higher in fish from the Kerguelen Plateau. Phleger *et al.* (1997) studying *E. antarctica* in the Antarctic, noted differences in fatty acid and alcohol composition for specimens from two locations. The same methodology was used in our study indicating that real variation in composition is apparent between studies. Whether this relates to the size and age of specimens, the site or year of capture and associated dietary differences presently remains unclear.

Inter-annual shifts in fatty acid composition may also occur as is evidenced by differences in profiles of mackerel icefish (*C. gunnari*) FA profiles from the same location, the vicinity of Heard Island, in the early 1990s (Nichols *et al.* 1994) and during this study. The combined level of the essential FA, EPA and DHA, was twofold higher in samples analysed by Nichols *et al.* (1994) with EPA/DHA comprising 52.5% of fatty acids, while the specimens examined in this study contained considerably higher proportions of 16:1ω7 (11.5% *cf* 4.3%) and 18:1ω9 (13.5% *cf* 6.4%). It appears, based on the FA composition of fish examined in this study, that significant inter-annual variations in dietary composition may occur for *C. gunnari* on the Kerguelen Plateau. This could indicate higher proportions of hyperiid amphipods such as *Themisto gaudichaudii* may comprise a large proportion of the diet in some years (e.g. elevated EPA and DHA) or in other years crustaceans such as *E. vallentini*,

the juveniles of which are known to be herbivorous (Gurney *et al.* 2001), may predominate. A recent study by Hunt *et al.* (2001) of the zooplankton community structure within the Polar Frontal Zone at the Prince Edward Islands confirms that the composition of zooplankton communities is highly spatially and temporally variable. Differences were due to hydrodynamic variability of the region, biological interactions and inter-annual variability in the timing of the biological season.

3.4.4 Conclusions

Myctophids constitute an important, energy-rich contribution to the diet of many Southern Ocean species and to date, many studies examining their composition have been limited by access to specimens and resultant low sample sizes. The findings presented here provide a basis, through the use of a signature lipid approach, for greater understanding of trophic links and energy transfer in the Southern Ocean, particularly in sub-Antarctic regions. It is evident from this study that much spatial and temporal variability exists in the biochemical composition of high latititude fish species and that further, broad-scale studies are required if we are to understand the links between more wide-ranging marine predators, such as whales and many seal species over the winter period, and their dynamic prey resources.

3.5 SUMMARY

- lipid content, fatty acid composition and calorific value of seven species of mesopelagic deep-sea fish of the family Myctophidae and the mackerel icefish, *Champsocephalus gunnari*, important in the diet of Southern Ocean marine predators were analysed
- fish were sampled at the Kerguelen Plateau (KP) and Macquarie Ridge (MR) in the Indian and Pacific sectors of the Southern Ocean respectively, to examine geographic variation in lipid compositon
- all species of myctophid from KP and *Electrona antarctica* (MR) were high in lipid content (6-18% wet mass), particularly *Gymnoscopelus nicholsi* (18%) and *E. antarctica* (15%)
- the mackerel icefish, *G. fraseri* and *Protomyctophum tenisoni* (MR) were generally lower in lipid content (3.4-5.2%) and varied significantly in fatty acid composition from KP species
- KP myctophids were high in calorific content (9.3 kJ g^{-1} wet mass) when compared with icefish (5.4 kJ g^{-1} wet mass) and other published values for prey items of marine predators such as squid (1.7-4.5 kJ g^{-1})
- KP myctophids could be distinguished from each other and from *C. gunnari* and MR specimens by cluster and discriminant function analysis using six fatty acids (16:0, 18:1ω9, 20:1ω9, 22:1ω11, 20:5ω3, 22:6ω3)
- findings presented here highlight trophic links between high latitude fish and their prey and emphasise the importance of myctophids as a significant energy source for marine predators foraging in the Polar Frontal Zone.

Chapter 4

Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from faecal and fatty acid analyses

4.1 Introduction[3]

The Southern Ocean ecosystem is strongly influenced by the movement of several strong currents, most notably the Antarctic Circumpolar current (ACC), and coupled climatic anomalies such as the Antarctic Circumpolar Wave (ACW, White and Peterson 1996). While primary production is relatively low in open parts of the Southern Ocean (Hempel 1985), frontal regions may form discrete areas of biological enhancement (Lutjeharms *et al.* 1985). Studies of zooplankton communities in the vicinity of the Antarctic Polar Frontal Zone (PFZ) have identified regions of high productivity that vary at a range of spatial and temporal scales (Pakhomov *et al.* 1994; Pakhomov and Froneman 2000; Hunt *et al.* 2001). Consequently the ecosystem also supports a very high biomass of vertebrate predators such as seals, penguins, and seabirds, which are limited in their distribution by their ability to travel from breeding sites while provisioning their offspring. Antarctic fur seals raise a single pup during a four-month lactation period from December to March during which they spend time foraging at sea followed by periods ashore suckling their pup (Doidge *et al.* 1986). As central place foragers they are limited in their prospecting range by the fasting constraints of their young and consequently, oceanographic variation within their foraging range could affect the species composition of prey available to them.

The Antarctic krill, *Euphausia superba*, comprises a large part of the zooplankton biomass in the Southern Ocean (Schnack 1985), providing a food source for a large proportion of marine predators south of the Antarctic Polar Front (PF), and in the vicinity of the Scotia Sea in particular (Croxall *et al.* 1985b; Reid 1995; Reid and Arnould 1996). Many sub-Antarctic predators however, such as King penguins, Antarctic fur seals, large pelagic fish and several species of squid (Sabourenkov 1991; Cherel and Ridoux 1992; Rodhouse and White 1995; Bost *et al.* 1997; Cherel *et al.* 1997; Goldsworthy *et al.* 1997; Green *et al.* 1997; Gonzàlez and Rodhouse 1998; Moore *et al.* 1998), depend primarily on mesopelagic fishes of the Family Myctophidae (lanternfishes) which represent the second largest and most widely distributed biological resource in Antarctic waters (Sabourenkov 1991), with many species being circumpolar in distribution (Hulley 1990).

The Kerguelen Archipelago in the southern Indian Ocean, is the summer breeding location of seabirds and seals, which in 1985 were estimated to consume approximately 462 000 tonnes of myctophids per year (Guinet *et al.* 1996), equating to 26% of all prey consumed. Two of the primary consumers, Antarctic fur seals (*Arctocephalus gazella;* Jouventin *et al.* 1982; Bester and Roux 1986) and King penguins *(Aptenodytes patagonicus)* have increased

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in number by up to seven fold in this vicinity over the last 35 years (Chamaillé-Jammes *et al.* 2000), and consequently annual consumption rates are now undoubtedly considerably higher than the 1985 estimate. Abundant and predictable prey resources are a necessary requirement to support growing predator populations. The Kerguelen Archipelago is within close proximity of the PF, lying in the southern part of the PFZ (Park and Gambéroni 1997), which is defined as the zone between the Sub-Antarctic Front (SAF) to the north and the PF to the south (Klyausov 1990; Park *et al.* 1993). The productive waters of the PFZ are likely to influence the foraging and breeding success of predators at Îles Kerguelen, in the absence of Antarctic krill, which are not found in the region (Bocher *et al.* 2001).

Myctophids, associated with deep Antarctic waters throughout their life cycles (Kozlov and Tarverdiyeva 1989), dominate the ichthyofauna within the southern PFZ near the Kerguelen Archipelago, with many species invading the surface layer at night (Duhamel *et al.* 2000) to feed on diurnally migrating meso- and macro-zooplankton. The general location of the ACC in this sector of the southern Indian Ocean is relatively stable owing to the influence of bottom topography (Park and Gambéroni 1995), however movements of the PF by several degrees of latitude between years occur intermittently (see Moore *et al.* 1999a). Thus, the relative proximity of the Kerguelen Archipelago to the PF provides an opportunity to examine inter-annual variation in diet of predators with respect to the effects of changing oceanographic features. Thus we aimed to document the diet of Antarctic fur seals breeding at Îles Kerguelen over three years with a larger aim of examining possible differences in diet with reference to variation in oceanographic conditions and the foraging behaviour of fur seals.

The majority of pinniped, and particularly otariid diet studies, have assessed prey composition by identifying hard parts, such as fish otoliths and squid beaks, remaining in faeces (Green *et al.* 1990; Daneri and Coria 1992; Reid and Arnould 1996; Cherel *et al.* 1997) and/or regurgitates (Goldsworthy 1992; Fea and Harcourt 1997; Kirkman *et al.* 2000). This method carries with it many biases in terms of the retention, digestion and erosion of prey hard parts. In feeding trials of several species of otariids, the recovery rates of otoliths have been found to be only 2-63% (Dellinger and Trillmich 1988; Gales and Cheal 1992; Fea and Harcourt 1997; Lake 1997), while a study of Antarctic fur seals identified high individual variability in recovery rates (0-90%; Staniland 2002), often with a complete absence of smaller fish otoliths (da Silva and Neilson 1985). In addition, hard parts actually retrieved from scats may only represent the ingestion of prey during the previous feeding bout (Helm 1984; Jobling and Breiby 1986; Staniland 2002). Several indirect methods are now being used to provide dietary information in addition to the conventional faecal

analyses. Lipids, particularly fatty acids (FA), may function as dietary indicators through the comparison of FA signatures of prey items with predator tissues high in lipid, such as milk (Iverson 1993; Iverson *et al.* 1997a; Brown *et al.* 1999), and adipose tissue (Grahl-Nielsen and Mjaavatten 1995; Raclot *et al.* 1998; Kirsch *et al.* 2000; Walton *et al.* 2000). This technique is based on the principle that unique arrays of fatty acids can be transferred largely unaltered up the food chain from prey to predator (Iverson *et al.* 1997a; Raclot *et al.* 1998).

A secondary aim of the study was to compare dietary changes estimated by conventional scat analysis with the findings of signature FA analysis (FASA) of fur seal milk samples. The life history characteristics of female Antarctic fur seals, which return regularly from their foraging grounds to feed their pups, make this species a good candidate to test comparisons of scat analysis and FASA. Fatty acids are derived primarily from dietary intake (Iverson *et al.* 1997b), and may represent dietary intake over a longer time span than scat analyses. Therefore, our secondary aim is to assess the usefulness of FA signature analysis (Iverson 1993) of fur seal milk in identifying longer-term dietary preferences than possible by conventional faecal analysis. TO achieve this aim, milk fatty acid signatures will be compared with fatty acid profiles of a selection of possible prey items (Chapter 3).

4.2 Materials and methods

4.2.1 Study site

The diet of female Antarctic fur seals breeding at Cap Noir, Îles Kerguelen (49°07'S, 70°45'E) was examined during February 1998, 1999 and 2000 (Fig. 4.1). The colony on the Northeastern coast of the Courbet Peninsula comprised approximately 800 breeding seals. Female seals typically arrive at the colony in late November and usually give birth to a single pup, which they then suckle until weaning in late March or early April. The female's time ashore is interspersed with trips to sea of several days duration to forage.

4.2.2 Faecal analyses

Faecal samples of lactating fur seals were collected within the colony from areas used by adult females, and from known seals upon their return to the colony whenever possible. Individual samples were frozen (-20°C) on site and returned to the laboratory for sorting and prey identification. Samples were elutriated overnight and subsequently sieved with a 1 mm and 500μm mesh. The frequency of occurrence (FO) of fish (otoliths and bones), squid (beaks and eye lenses), invertebrates (amphipods, isopods, nematodes and annelids) and other miscellaneous items in faeces was noted. Percentage FO is expressed as a proportion of the number faeces containing prey items. Otoliths (sagitta, asteriscus and lapillus) and squid beaks were sorted and identified to species level if possible, using the descriptions in Clarke

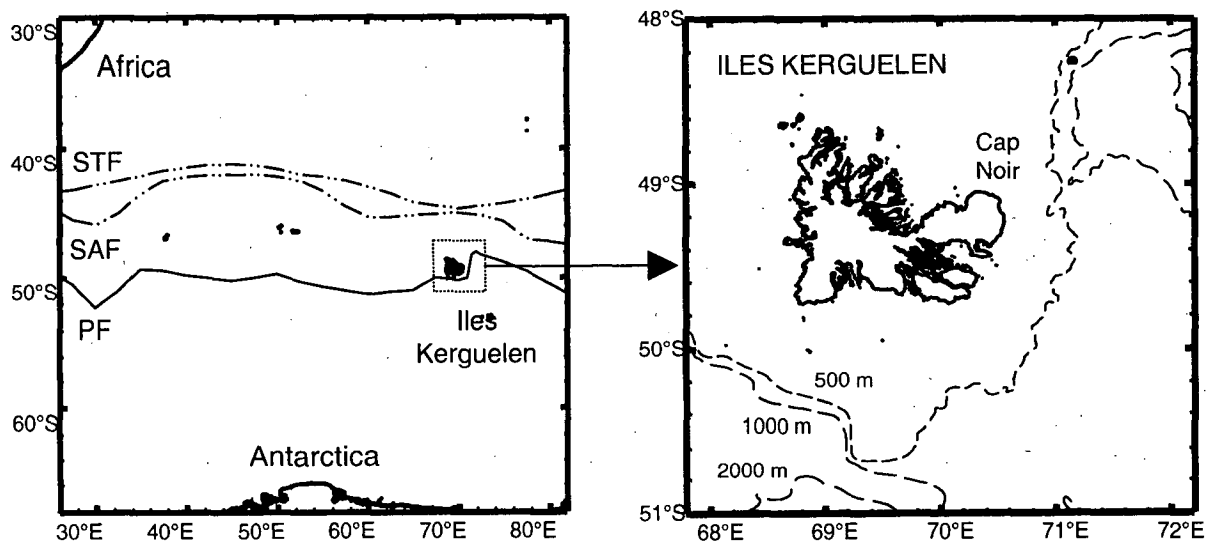


Figure 4.1 Locational map of Îles Kerguelen and oceanographic fronts of Southern Ocean (STF=sub-tropical front; SAF=sub-Antarctic front; PF= Polar Front).

(1986), Williams and McEldowney (1990), Reid (1996) and our own reference collection at the CEBC (France). Subsequently, otolith length was measured from otoliths showing little or no sign of erosion. Standard length and biomass of fish species were calculated from the conversion of otolith length (mm) using allometric equations (Adams and Klages 1987; Williams and McEldowney 1990; Cherel *et al.* 1997; Olsson and North 1997) for the majority of species. The conversion of lower rostral length to mantle length and squid body mass was achieved using allometric equations from Clarke (1986), Rodhouse *et al.* (1990) and (Jackson 1995). In reconstructing the estimated fish biomass consumed by fur seals from scats, each otolith was considered to represent one fish as there is little chance of all fish, and therefore otoliths consumed by the seal being present in a particular scat. Calculations of the mean numbers of otoliths per scat were made using only those scats conatining otoliths.

4.2.3 Dietary energy value

The mean energetic value of the prey in each scat for the 3 years was estimated using the calorific value of prey items (kJ g^{-1} wet mass). An estimate of the calorific content of the 8 major species of fish prey from the Kerguelen Plateau was available from Chapter 3, and for other species of myctophid from Tierney *et al.* (2002) and Cherel and Ridoux (1992). In instances where the calorific value of a particular species was unknown an average value was used for that genus or class. A value of 5.4 kJ g^{-1}, that of *Champsocephalus gunnari* from the Kerguelen Plateau, was assigned to other non-myctophid fish prey in the absence of further data. The calorific content of *Gonatus antarcticus* (3.78 kJ g^{-1}) was taken from Clarke *et al.* (1985) and a value of 2.31 kJ g^{-1} was used for ammoniac squids and 4.25 kJ g^{-1} for muscular squids Clarke *et al.* (1985).

4.2.4 Fatty acid analyses

Milk samples were collected from breeding female fur seals captured for the deployment or retrieval of time-depth recorders in February 1999 and 2000 (Chapter 2), usually within 24 hours of the female's arrival in the colony. The seals were injected with 1mL of 10 IU Oxytocin (Herriot Agvet, Australia) intramuscularly upon capture. The milk was then manually extracted into two 2mL vials and frozen immediately at -20°C. In the laboratory, the milk samples were thawed, mixed and weighed.

The lipid was quantitatively extracted overnight by a modified (Bligh and Dyer 1959) one-phase methanol/chloroform/water extraction. The phases were separated the following day by the addition of chloroform, water and sodium chloride. Concentration of the total solvent extract (TSE) was obtained by *in vacuo* rotary evaporation at 40°C. A sub-sample of the extracted lipid was made up to a known concentration by the addition of chloroform and stored in the freezer (-20°C). Lipid class analyses were conducted immediately; samples

were stored for no more than three days in a known volume of chloroform. The quantity of lipid extracted per sample was used to calculate percentage lipid values.

An aliquot of the total lipid was analyzed using an Iatroscan MK V TH10 thin-layer chromatography–flame-ionization detector (TLC–FID) analyzer (Tokyo, Japan) to determine the abundance of individual lipid classes (Volkman and Nichols 1991). Peaks were quantified on an IBM compatible computer using DAPA software (Kalamunda, Western Australia). Iatroscan results are generally reproducible to ±10% (Volkman and Nichols 1991).

An aliquot of the total lipid was treated with methanol/hydrochloric acid/chloroform (10:1:1, by vol; 80°C, 2 h). The fatty acid methyl ester (FAME) products were extracted into hexane/chloroform (4:1, vol/vol, 3 x 1.5 ml) and after reduction under a stream of nitrogen the FAME mixture was treated with N,O-bis-(trimethylsilyl)-trifluoroacetamide (BSTFA, 50 µl, 60°C, 1 h) to convert sterols to their corresponding TMSi (trimethylsilyl) ethers. Gas chromatographic (GC) analyses of methyl esters of fatty acids were performed with a Hewlett Packard 5890A GC (Avondale, PA) equipped with an HP-5 cross-linked methyl silicone fused silica capillary column (50 m x 0.32 mm i.d.), an FID, a split/splitless injector and an HP 7673A auto sampler. Hydrogen was the carrier gas. Following addition of methyl nonadecanoate and methyl tricosanoate internal standards, samples were injected in splitless mode at an oven temperature of 50°C. After 1 minute, the oven temperature was raised to 150°C at 30°C min^{-1}, then to 250°C at 2°C min^{-1} and finally to 300°C at 5°C min^{-1}.

Peaks were quantified with Waters Millenium software (Milford, MA, USA). Individual components were identified using mass spectral data and by comparing retention time data with those obtained for authentic and laboratory standards. GC results are subject to an error of ± 5% of individual component abundance.

4.2.5 Statistical analyses

All parametric statistical tests were performed using SYSTAT 9.0 (SYSTAT Inc., Illinois, USA). Inter-annual comparisons, of fish prey abundance identified from faecal analyses, were conducted by Discriminant Function Analysis (DFA) of log+1 transformed abundance data. Otoliths not identified to species due to erosion were excluded. A backwards-stepwise DFA (alpha level of 0.05 to remove) identified those species most influential in distinguishing the fish diet between years.

An analysis of covariance (ANCOVA) was performed on arcsine transformed monounsaturated (MUFA) and polyunsaturated (PUFA) proportions for 1999 and 2000. Data

were weighted according to MUFA proportions to account for the correlation between variables. Otherwise, the percentages of fatty acids identified in milk samples were compared inter-annually by t-test after arcsine transformation of the data and a Bonferroni correction (Zar 1996) was applied to the significance level ($P<0.0014$) to account for multiple comparisons and the possibility of significance occurring by chance. Those fatty acids identified as significantly different between years were then incorporated in a backwards-stepwise DFA on arcsine transformed proportion data to identify those fatty acids most important in differentiating between milk samples from different years. Fatty acid profiles of milk samples were compared with profiles of 12 possible prey species from the literature. We selected species present in the diet of fur seals at Îles Kerguelen, which were sampled from the Kerguelen Plateau region where possible, to compare inter-annual variation in diet between the two techniques. All values are reported as ± SEM.

4.3 Results

A total of 131 scats were collected in February over the three-year study, 60 in 1998, 24 in 1999 and 47 in 2000. Of those 131 scats, 83.2% contained fish otoliths (1998:55; 1999: 21; 2000: 33). Fish comprised the majority of the diet in terms of FO in all three years (Table 4.1) with FO ranging from 90.9 to 94.9% of samples. Squid, while present in lower absolute numbers, were also found in the majority of scat samples (62.5-72.9%). The presence of several species of crustaceans such as the amphipod *Themisto gaudichaudii* was evident from exoskeletons found in the faecal remains (Table 4.1). Nematodes were also common in samples, while small quantities of plastic were also present in 9.1% of scats sampled in 2000.

4.3.1 Fish prey

In total, 3608 sagittal otoliths were found during the study at average of 38±33 otoliths per scat (range 1-215). Otoliths from 25 fish species were identified in the scats over the three years (1998-2000), 16 of which were Myctophidae. *Gymnoscopelus piabilis*, *Electrona subaspera* and *G. nicholsi* accounted for 54.7% by number of the fish prey species identified in the mean diet of the fur seals (Table 4.2). A further 20.3% of otoliths were from the Genus *Gymnoscopelus* or the family Myctophidae and were too eroded to reliably identify. An average 90.4% by number of the diet, as assessed by prey hard parts, consisted of myctophid fish. Other species of fish accounted for 7.5% of prey items by number with *Champsocephalus gunnari*, the mackerel icefish, being the most numerous of these (4.4%). *Harpagifer spinosus*, *Scopelosaurus hamiltoni* and the southern driftfish, *Icichthys australis*, followed in numerical abundance, all at less than 1%.

4.3.2 Cephalopod prey

Six species of squid were found in the diet, with squid remains occurring in 67.7% of scat samples (Table 4.2). The ommastrephid squid *Martialia hyadesi,* and *Brachioteuthis ?riisei* occurred most commonly, whilst *Gonatus antarcticus, Moroteuthis ingens, M. knipovitchi* and *?Mastigoteuthis A* (Clarke) were also present in lower numbers (Table 4.2). The squid component of the diet comprised, on average, only 2.1% of the diet by number.

Table 4.1: Frequency of occurrence by number and percentage of prey items recorded in Antarctic fur seal scats in February at Cap Noir. Number of scats sampled and the number containing prey items are in parentheses.

Prey type	1998 (60/59)		1999 (24/24)		2000 (47/44)		Total (132/127)	
	n	%	n	%	n	%	n	%
Fish	56	94.9	22	91.7	40	90.9	118	92.9
Otoliths	55	93.2	21	87.5	33	75.0	109	85.8
Eye lenses	52	88.1	18	75.0	31	70.5	101	79.5
Bones	48	81.4	20	83.3	37	84.1	105	82.7
Vertebrae	49	83.1	16	66.7	26	59.1	91	71.7
Myctophids (scales or jaw bones)	39	66.1	17	70.8	34	77.3	90	70.9
Channichthyids (jaw bones or opercles)	13	22.0	1	4.2	0	0	14	11.0
Nototheniids (jaw bones)	7	11.9	1	4.2	6	13.6	14	11.0
Paradiplospinus gracilis (teeth or vertebrae)	4	6.8	1	4.2	0	0	5	3.9
Harpagifer spinosus (opercles)	1	1.7	0	0.0	1	2.3	2	1.6
Cephalopods	43	72.9	15	62.5	28	63.6	86	67.7
Beaks	36	61.0	14	58.3	25	56.8	75	59.1
Eye lenses	30	50.9	8	33.3	20	45.5	58	45.7
Gladii	22	37.3	8	33.3	17	38.6	47	37.0
Radulae	13	22.0	9	37.5	11	25.0	33	26.0
Crustaceans	25	42.4	13	54.2	11	25.0	49	38.6
Themisto gaudichaudii	18	30.5	5	20.8	5	11.4	28	22.1
Other amphipods	9	15.3	6	25.0	0	0.0	15	11.8
Isopods	2	3.4	1	4.2	1	2.3	4	3.2
Euphausiacae	1	1.7	0	0.0	0	0.0	1	0.8
Others								
Nematodes	33	55.9	18	75.0	27	61.4	78	61.4
Pebbles	18	30.5	16	66.7	23	52.3	57	44.9
Mollusk shells	11	18.6	12	50.0	4	9.1	27	21.3
Plastic	1	1.7	1	4.2	4	9.1	6	4.7
Annelids	4	6.8	0	0.0	0	0.0	4	3.2
Feathers (penguin)	1	1.7	0	0.0	0	0.0	1	0.8

4.3.3 Inter-annual variation in number and size of prey

The number of fish and squid species identified in the diet of seals was highest in 1998 at 33 species, with 21 and 22 species in 1999 and 2000 respectively. A prey diversity index was

Table 4.2: Mean abundance by number of fish (otoliths) and squid prey (lower beaks) in the diet of female Antarctic fur seals at Îles Kerguelen. Sample size and samples containing prey remains in parentheses.

	1998 (60/55)			1999 (24/21)			2000 (47/33)			Total (131/109)		
	Number		%	Number		%	Number		%	Number		%
Myctophidae	n	%	Fish	n	%	Fish	n	%	Fish	n	%	Fish
Gymnoscopelus piabilis	461	28.5	29.2	219	21.3	21.6	280	26.8	27.6	960	26.0	26.6
Electrona subaspera	269	16.6	17.1	194	18.9	19.1	192	18.4	18.9	655	17.8	18.2
Gymnoscopelus nicholsi	152	9.4	9.6	92	9.0	9.1	159	15.2	15.6	403	10.9	11.2
Gymnoscopelus fraseri	61	3.8	3.9	42	4.1	4.1	53	5.1	5.2	156	4.2	4.3
Protomyctophum bolini	46	2.8	2.9	16	1.6	1.6	19	1.8	1.9	81	2.2	2.2
Protomyctophum choriodon	39	2.4	2.5	57	5.6	5.6	18	1.7	1.8	114	3.1	3.2
Electrona carlsbergi	26	1.6	1.6	0			0			26	0.7	0.7
Krefftichthys anderssoni	24	1.5	1.5	20	1.9	2.0	3	0.3	0.3	47	1.3	1.3
Electrona antarctica	19	1.2	1.2	62	6.0	6.1	11	1.1	1.1	92	2.5	2.5
Gymnoscopelus sp.	131	8.1	8.3	130	12.7	12.8	197	18.9	19.4	458	12.4	12.7
Myctophidae (eroded)	97	6.0	6.2	137	13.4	13.5	42	4.0	4.1	276	7.5	7.6
Metelectrona ventralis	11	0.7	0.7	0			1	0.1	0.1	12	0.3	0.3
Protomyctophum tenisoni	9	0.6	0.6	20	1.9	2.0	3	0.3	0.3	32	0.9	0.9
Gymnoscopelus braueri	1	0.1	0.1	0			0			1	0.0	0.0
Protomyctophum andriashevi	1	0.1	0.1	1	0.1	0.1	0			2	0.1	0.1
Gymnoscopelus bolini	2	0.1	0.1	2	0.2	0.2	13	1.2	1.3	17	0.5	0.5
Other fish												
Champsocephalus gunnari	161	10.0	10.2	0			0			161	4.4	4.5
Harpagifer spinosus	23	1.4	1.5	2	0.2	0.2	2	0.2	0.2	27	0.7	0.7
Icichthys australis	10	0.6	0.6	7	0.7	0.7	0			17	0.5	0.5
?Nansenia antarctica	7	0.4	0.4	3	0.3	0.3	0			10	0.3	0.3
Scopelosaurus hamiltoni	7	0.4	0.4	8	0.8	0.8	5	0.5	0.5	20	0.5	0.6
Osteichthyes sp., (eroded)	7	0.4	0.4	0			4	0.4	0.4	11	0.3	0.3
Paradiplospinus gracilis	3	0.2	0.2	3	0.3	0.3	0			6	0.2	0.2
Gobionotothen acuta	4	0.2	0.3	0			13	1.2	1.3	17	0.5	0.5
Paralepididae sp.	1	0.1	0.1	0			0			1	0.0	0.0
Muraenolepis marmoratus	2	0.1	0.1	0			0			2	0.1	0.1
Melanostigma gelatinosum	2	0.1	0.1	0			0			2	0.1	0.1
Notothenia cyanobrancha	1	0.1	0.1	0			1	0.1	0.1	2	0.1	0.1
Total otoliths	1577	97.5	100	1015	99.0	100	1016	97.3	100	3608	97.9	100
Squid												
Martialia hyadesi	23	1.4		1	0.05		15	1.4		39	1.1	
Brachioteuthis ?riisei	11	0.7		9	0.9		11	1.1		31	0.8	
Gonatus antarcticus	3	0.2		1	0.05		0			4	0.1	
Moroteuthis ingens	1	0.1		0			0			1	0.0	
M. knipovitchi	1	0.1		0			1	0.1		2	0.1	
?Mastigoteuthis A (Clarke)	0			0			1	0.1		1	0.0	
Total squid beaks	39	2.5		11	1.0		28	2.7		78	2.1	
TOTAL	1616	100		1026	100		1044	100		3686	100	

calculated on an individual scat basis (number of fish and squid species groups per scat) and averaged for each year. The prey index did not vary significantly between years (5.4±0.3, n=110, range 1-13) for those scats containing diagnostic hard parts (one-way ANOVA, $F_{107,2}$=2.037, P=0.135). However, if the prey indices for all scats were used, i.e. including those scats with no prey, the index was significantly lower in 2000 (3.2±0.5, one-way ANOVA, $F_{129,2}$=6.027, P<0.05) than in 1998 and 1999 (4.9±0.4 and 5.8±0.8 respectively). The high proportion of empty scats in 2000 (31.3%), as opposed to other years (both 8.3%), explains this finding.

4.3.3.1 Fish

Myctophids comprised 85.6, 97.8 and 97.6% of the fish component of the diet in each of the three years respectively ($\bar{x}$=93.7%). *Gymnoscopelus piabilis* was the main prey species consumed in all years (Table 4.2). Similar proportions of the three most common fish prey species (*G. piabilis, G. nicholsi* and *E. subaspera*) were consumed by seals in all years, although *G. nicholsi* was more prevalent in the diet in 2000 than in 1998 and 1999. The importance of some of the minor prey species varied considerably between years. The mackerel icefish, *C. gunnari,* was of variable importance in the diet, only being present in 1998 where it represented approximately 10% by number (Table 4.2). *E. carlsbergi* also occurred only in 1998 while *Protomyctophum choriodon* and *P. tenisoni* were present in higher numbers in 1999. The mean number of otoliths per scat (33.4±3.65) did not vary significantly between years (one-way ANOVA, $F_{2,105}$=2.123, P=0.125) with considerable variation occurring in numbers of otoliths between scats (1-215).

An inter-annual difference in dietary composition was detected by a complete linear DFA of log transformed abundance data (Wilks' Lambda = 0.4519, Approx. $F_{48,162}$=1.6455, P =0.012). The canonical scores plot indicates a high degree of overlap occurs between years, particularly in 2000 (Fig. 4.2). A backwards-stepwise DFA conducted on the same data indicated that two species, *P. tenisoni* and *Champsocephalus gunnari,* were largely responsible for the distinction in diet between years (Wilks' Lambda = 0.7941, Approx. $F_{4,206}$ = 6.2916, P=0.0001). Using these two species as discriminators, an average 44% of scats were correctly assigned to the year by the Jackknife classification matrix (Table 4.3). The fact that 90% of samples collected in 2000 were correctly assigned, in comparison to the lower percentages for 1998 (22%) and 1999 (33%) indicates that although differences between years were evident, a core diet was present in all years and comprised the majority of the diet in 2000 (Fig. 4.2). The difficulty in ascribing a scat sample to the correct year in 1998 and 1999 exemplifies the variability inherent in the samples.

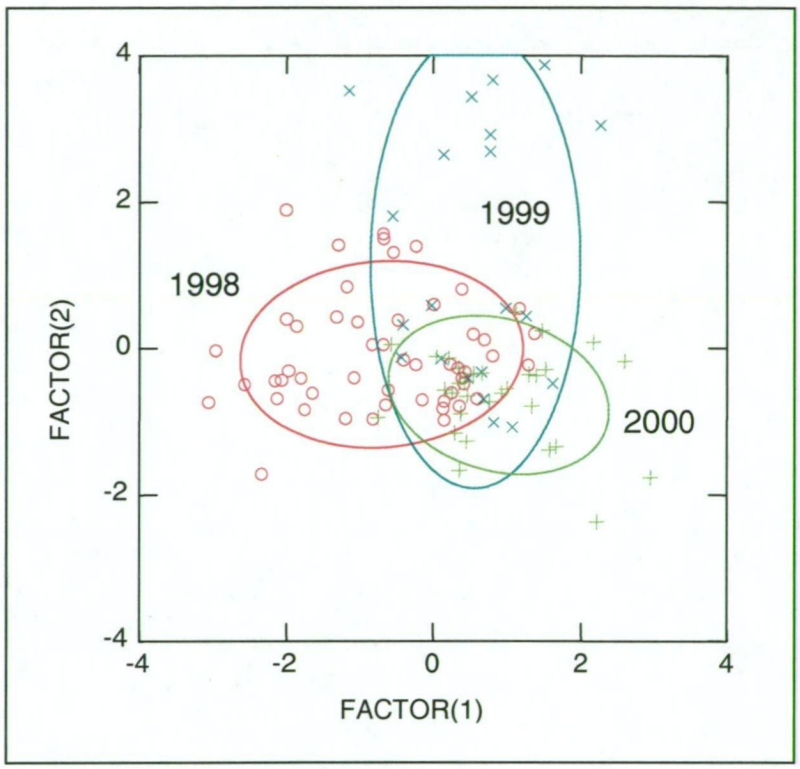


Figure 4.2 Canonical scores plot of prey species composition by number in 1998 (o), 1999 (x) and 2000 (+).

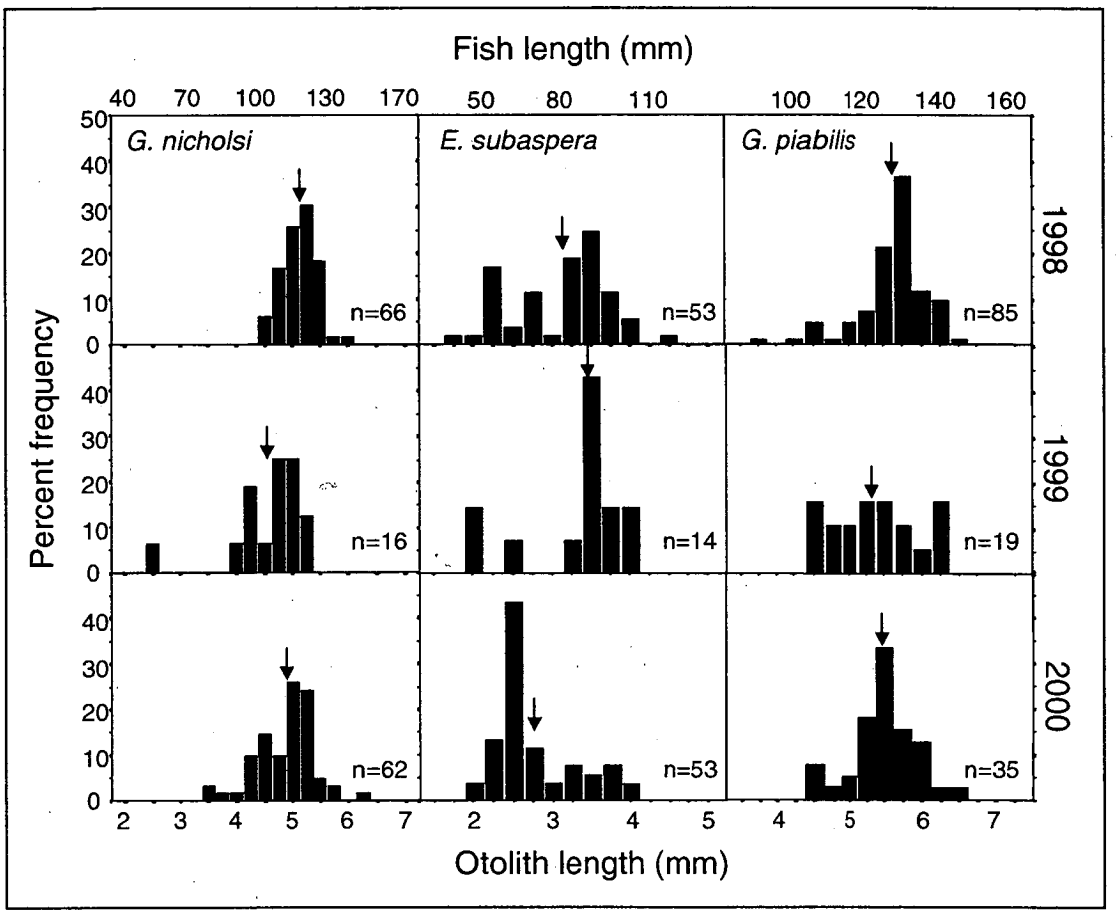


Figure 4.3 Percent frequency histograms of otolith and total fish length for *Gymnoscopelus piabilis*, *G. nicholsi* and *E. subaspera (*arrows denote mean otolith or fish length*)*.

Otolith sizes of the three most common species of fish prey (Fig. 4.3), were compared between years by one-way ANOVA. *Gymnoscopelus nicholsi* were smaller in 1999 than in 1998 and 2000 ($F_{2,145}$=13.104, P<0.001), *E. subaspera* were larger in 1999 than in 2000 while fish consumed in 1998 were intermediate ($F_{2,117}$=7.549, P=0.001). *Gymnoscopelus piabilis* were similar in size in all years (Table 4.4), although the distribution of fish sizes in 1998 was skewed more toward fish of greater than 120 mm. The majority of myctophid fish preyed upon by *A. gazella* were juveniles excepting *G. piabilis* in all years and *E. antarctica* and *P. tenisoni* in 2000.

Table 4.3: Discriminant function analysis stepwise (SCM) and Jackknife (JCM) classification matrices of fish abundance by number in 1998, 1999 and 2000

		1998	1999	2000	%correct
SCM	1998	13	5	37	24
	1999	0	7	14	33
	2000	0	3	28	90
	Total	13	15	79	45
JCM	1998	12	6	37	22
	1999	0	7	14	33
	2000	0	3	28	90
	Total	12	16	79	44

Champsocephalus gunnari consumed in 1998 ranged in size from 175.3 to 210.1 mm ($\bar{x}$=192.9±9.8 mm) indicative of fish at age 1+ from the September 1996 cohort (Guy Duhamel Personal Communication).

4.3.3.2 Cephalopods

The overall abundance of squid was generally low, however of the two more prevalent species, *M. hyadesi* occurred in 1998 and 2000 in similar proportions (1.4%), whilst *B. ?riisei* was present in all years at 0.7-1.1% of the diet.

Lower rostral lengths (LRL) of *M. hyadesi* squid beaks were compared between 1998 (3.74±0.4 mm) and 2000 (4.33±0.5 mm) by Student's *t*-test as only one individual was present in 1999. Beaks of *M. hyadesi* were significantly larger in 2000 than those consumed in 1998 ($t_{36[0.05]}$=2.042, P <0.001). The LRL of *B. ?riisei* were compared in all 3 years by ANOVA with squid in 1998 (LRL=2.43±0.5mm) being significantly larger than those in 2000 (LRL=1.8±0.5 mm; $F_{2,30}$=5.109, P <0.05), while the length of *B. ?riisei* taken in 1999 was intermediate (LRL=2.02±0.4 mm; Table 4.4).

Table 4.4: Size, reconstituted mass and energy value of the major fish and squid prey items in the diet of Antarctic fur seals (*length (L) = standard L for fish and mantle L for squid).

	1998						1999						2000					
	Mean Length*	Mass	Total Biomass		Energy Content		Mean Length	Mass	Total Biomass		Energy Content		Mean Length	Mass	Total Biomass		Energy Content	
Myctophidae	mm	g	g	%	kJ	%	mm	g	g	%	kJ	%	mm	g	g	%	kJ	%
Electrona antarctica	65.3	4.7	89	0.2	1181	0.4	51.9	2.1	127	0.7	1693	1.3	73.3	5.6	62	0.3	827	0.5
Electrona carlsbergi	80.2	7.8	202	0.5	1737	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Electrona subaspera	77.9	10.2	2743	6.4	20295	7.4	83.7	12.5	2425	12.7	17945	13.7	67.5	6.5	1248	5.7	9235	6.0
Gymnoscopelus fraseri	75.7	5.0	305	0.7	3113	1.1	74.7	4.9	206	1.1	2105	1.6	78.1	5.6	295	1.4	3013	2.0
Gymnoscopelus nicholsi	122.0	20.4	3107	7.2	30445	11.1	103.9	13.7	1264	6.6	12384	9.5	115.9	17.9	2844	12.9	27868	18.1
Gymnoscopelus piabilis	129.7	26.4	1217	28.3	83976	30.6	124.2	23.4	5125	26.9	35360	27.1	127.4	25.0	7000	32.0	48300	31.4
Gymnoscopelus bolini	186.7	71.8	144	0.3	1292	0.5	177.5	64.4	129	0.7	1160	0.9	190.8	78.5	1020	4.7	9182	6.0
Gymnoscopelus braueri	95.9	7.9	8	0.02	71	0.03	-	-	-	-	-	-	-	-	-	-	-	-
Gymnoscopelus sp.	128.3	25.6	3354	7.8	23145	8.4	128.3	25.6	3329	17.5	22969	17.6	128.3	25.6	5044	23.0	34806	22.6
Krefftichthys anderssoni	34.0	0.4	10	0.02	78	0.03	32.5	0.3	6	0.03	49	0.04	39.0	0.7	2	0.01	17	0.01
Myctophidae (eroded)	74.0	8.8	858	2.0	6349	2.3	74.0	8.8	1212	6.4	8967	6.9	74.0	8.8	371	1.7	2749	1.8
Metelectrona ventralis	69.0	5.3	58	0.1	769	0.3	-	-	-	-	-	-	69.0	5.3	5	0.02	70	0.05
Protomyctophum bolini	40.7	0.9	43	0.1	245	0.1	40.3	0.9	15	0.1	83	0.06	38.8	0.8	16	0.07	89	0.06
Protomyctophum andriashevi	51.2	8.4	8	0.02	51	0.02	51.2	8.4	8	0.04	51	0.04	-	-	-	-	-	-
Protomyctophum choriodon	67.8	4.3	170	0.4	1034	0.4	68.5	4.7	268	1.4	1632	1.3	64.2	3.6	65	0.3	394	0.3
Protomyctophum tenisoni	42.6	0.8	7	0.02	42	0.02	35.0	0.4	8	0.04	51	0.04	47.1	1.1	3	0.01	19	0.01
Total Myctophidae				54.1		63.3				74.1		79.9				82.1		88.8
Champsocephalus gunnari	129.9	47.5	7648	17.8	41297	15.0	-	-	-	-	-	-	-	-	-	-	-	-
Icicthys australis	318.1	620.9	6209	14.4	33527	12.2	318.1	620.9	4346	22.8	23469	18.0	-	-	-	-	-	-
Other fish	-	-	1618	3.8	8736	3.2	-	-	358	1.9	1935	1.4	-	-	659	3.0	3560	2.3
Squid																		
Martialia hyadesi	212.1	158.8	3652	8.5	15523	5.7	220.5	182.1	182	1.0	774	0.6	229.5	213.7	3206	14.6	13623	8.9
Brachioteuthis ?riisei	65.3	6.1	67	0.2	155	0.1	57.1	4.7	42	0.2	98	0.1	52.9	4.1	45	0.2	104	0.1
Gonatus antarcticus	143.9	71.6	215	0.5	812	0.3	27.0	0.6	1	0.0	2	0.0	-	-	-	-	-	-
Moroteuthis ingens	164.5	140.5	141	0.3	325	0.1	-	-	-	-	-	-	-	-	-	-	-	-
M. knipovitchi	91.8	163.0	163	0.4	377	0.1	-	-	-	-	-	-		1.9	2	0.01	4	0.0
?Mastigoteuthis A (Clarke)	-	-	-	-	-	-	-	-	-	-	-	-	76.5	14.4	14	0.07	26	0.02
TOTAL			42987	100	274572	100			19051	100	130726	100			21902	100	153888	100
Biomass or energy per scat			772±102		4799±674				865±221		5942±1549				673±120		4712±838	

4.3.4 Reconstituted mass and calorific value of prey

Myctophids also dominated the diet in terms of reconstituted mass, accounting for 54%, 74% and 82% of biomass in 1998, 1999 and 2000 respectively. In total, the three most commonly occurring species (*G. piabilis, G. nicholsi* and *E. subaspera*) represented 42-51% of the reconstituted mass, whilst *G. piabilis* alone consistently represented approximately 30% of biomass (Table 4.4). Some species accounted for a considerably higher proportion of the diet in terms of reconstituted mass than by number, such as the mackerel icefish (17% *cf.* 10%) and the Southern driftfish, *Icicthys australis* in 1999 (22% *cf.* 0.7%) owing to their large size (mean mass 620g).

Although reconstituted biomass and energy content of the diet are not quantitative measures, particularly when calculated from faecal remains, inter-annual comparisons of these measures are of interest. Prey biomass per scat (763±77 g) did not differ between years when compared by one-way ANOVA ($F_{2,105}$=0.382, P=0.683). Prey energy value per scat was similar between years (one-way ANOVA, $F_{2,105}$=0.368, P =0.693) at 5070±522 kJ, with much variation evident between scats (33-33674 kJ). Energy value per scat was positively related to the reconstituted mass per scat for all three years (r^2=0.901-991, P <0.05). The slopes of the relationship were tested for year effects by ANCOVA. Scats in 1998 constituted less energy per gram of reconstituted prey biomass than those from 1999 and 2000 ($F_{2,104}$=2.910, P =0.059).

4.3.5 Milk lipid and fatty acid analyses

Antarctic fur seal milk is generally rich in lipid content ranging from 28.1% to 68.7% of wet mass. The mean lipid content of milk sampled during late lactation 1999 (43.3±7.1%, n=22) was significantly lower than the 53.2±6.8% recorded in 2000 (n=16, $t_{36[0.05]}$=-4.361 pooled variance, P <0.001). Lipid class analyses of 20 milk samples indicated that milk was comprised of a minimum 99% triacylglycerides (TAG) and small amounts of polar lipid and sterols. The major fatty acids in Antarctic fur seal milk were 18:1ω9 (25-38%), 16:0 (15-23%), 20:1ω9 (6-11%), 22:6ω3 (1-10%), 16:1ω7 (5-8%), 20:5ω3 (1-8%) and 18:1ω7 (4-7%). Monounsaturated fatty acids (MUFAs, 50-63%) were more prevalent than either polyunsaturated fatty acids (PUFAs, 6-24%) and saturated fatty acids (22-33%).

4.3.5.1 Intra-individual variation in milk lipid composition

To evaluate the possibility of short-term temporal variation in milk fatty acid composition, the fatty acid profiles of milk samples collected before and after one or two foraging trips for 13 females were compared. A Pearson's Correlation Co-efficient was calculated for each pair of milk samples and regressed against the number of days between milk samples (Fig. 4.4 a.&b.). The correlation between fatty acid composition of pre- and post-foraging trip

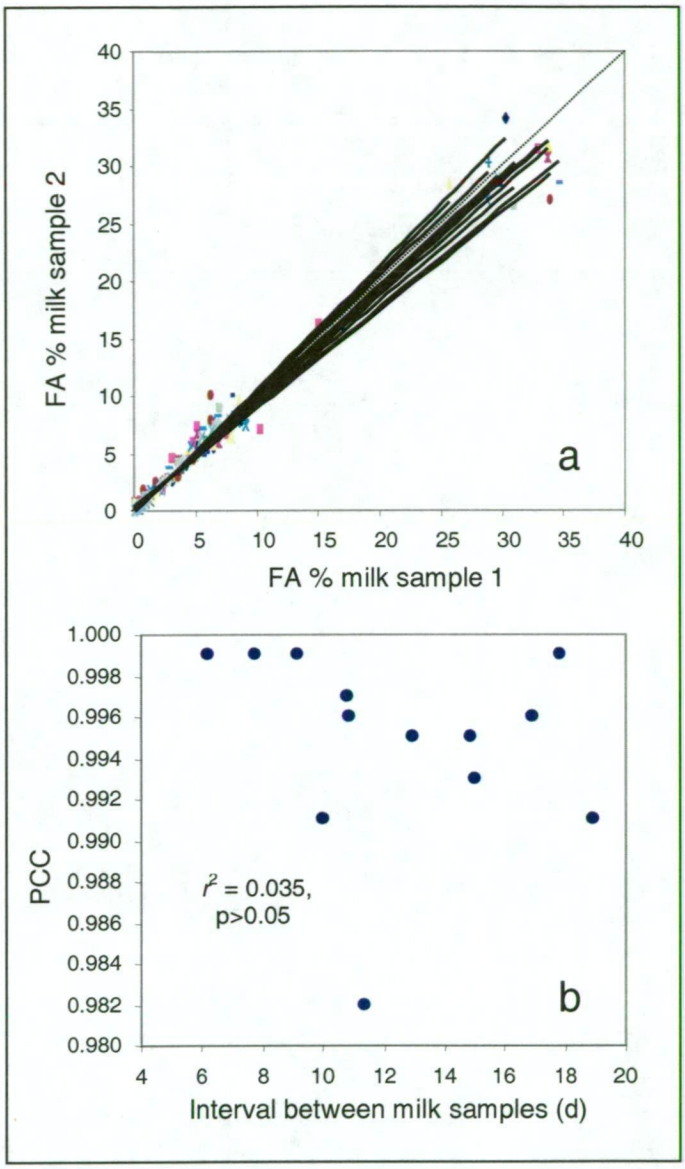


Figure 4.4 (a) Correlation between paired milk samples from 13 Antarctic fur seals (dotted line 1:1 slope); and *(b)* regression of Pearson's Correlation Co-efficient (PCC) against sampling interval between milk sample collections.

milk samples, was high (mean PCC=0.995±0.005). However no relationship was apparent between the number of days between samples, which ranged between 7.8 and 18.9 days (r^2=0.035, P >0.05) and the r correlation co-efficient. Thus it would appear there is little intra-individual variation in milk fatty acid composition over a 1 to 3 week time span.

4.3.5.2 Inter-annual variation in milk fatty acid profiles

The fatty acid profiles of seal milk in February/March 1999 (n=22) and 2000 (n=16) were variable both within and between years, with the proportion of 19 fatty acids present in milk samples differing between the two years when tested by t-test (Table 4.5). The relationship between MUFA and PUFA levels in the two years was significantly different (ANCOVA, $F_{35,1}$=22.354, P<0.05) with milk samples higher in PUFAs in 1999 (21.4%), while in 2000 milk was more variable in composition with several seals having a particularly high occurrence of MUFAs (Fig. 4.5). In 1999, relative proportions of 22:6ω3 (DHA) overall PUFA levels were higher than in 2000 (see Table 4.5 for test-results). Whilst the abundance of saturated fatty acids and 16:1ω7, 18:1ω7 and 20:1ω9 was greater in 2000 (Table 4.5). The ratio of essential ω6 to ω3 fatty acids (6.1±0.63) was significantly lower in 2000 than in 1999 (7.9±0.4; $t_{36[0.05]}$=2.632, P <0.5).

4.3.5.3 Dietary implications of fatty acid analysis

The proportional abundance of 19 fatty acids in the milk samples differed significantly between years (Table 4.5). Of those 19 fatty acids, nine were identified by a backwards-stepwise DFA (i15:0, 15:0, 16:1ω5, 18:1ω7, 20:1ω9, 20:1ω7, C_{21}PUFA, DPA6 and 22:6ω3) as contributing to a significant inter-annual difference between milk samples (Wilks' Lambda=0.1174, Approx. $F_{9,28}$=23.3997, P <0.0001). Samples from the different years were correctly re-assigned to year in 100% of cases using both a standard classification matrix and a Jackknife classification matrix.

The relative abundance of the nine influential fatty acids identified by DFA were compared between the 12 potential prey items which included three species of squid: *Martialia hyadesi* (SP); *Moroteuthis knipovitchi* (HI) and *Gonatus antarcticus* (HI) from the Southern Plateau (SP) and Heard Island (HI; K. Phillips *et al.* Unpublished data); seven species of myctophid (*E. carlsbergi; E. subaspera; G. piabilis; G. fraseri, G. nicholsi*; *P. tenisoni*) and *Champsocephalus gunnari* from the Kerguelen Plateau (Chapter 3) and the crustacean *Themisto gaudichaudii* (Phleger *et al.* 1998) from the Elephant Island region, Antarctica. The relative proportions of six of the fatty acids were higher in milk samples in 2000 (Table 4.6). The fatty acid *i*15:0, for which the highest t value was recorded in inter-annual comparisons of milk samples, was highest in two of the common fish prey species (*G. piabilis* and *E. subaspera*) in addition to *G. fraseri* and *P. tenisoni* (Chapter 3), however it was present only

at very low levels (<0.5%) in milk samples (Table 4.5). The monounsaturated 18:1ω7 fatty acid was unique in that the only prey item with high levels of this fatty acid was *G. nicholsi* which was more common in the diet of seals in 2000 (13.3%) in terms of prey biomass than in 1999 (6.6%). Both 20:1ω9 and 20:1ω7 were also indicative of *G. nicholsi* to a lesser extent.

Table 4.5: Fatty acid composition (% wet mass) of Antarctic fur seal milk in late lactation 1999 & 2000. Values are mean ± SE.

Fatty acids	1999	2000	*t*	*p*
14:0	3.69 ± 0.11	4.56 ± 0.20	4.156	0.0001
15:0	0.33 ± 0.01	0.38 ± 0.02	3.458	0.001
16:0	16.53 ± 0.10	18.63 ± 0.52	4.639	0.0001
18:0	2.79 ± 0.04	3.35 ± 0.11	5.517	0.0001
20:0	0.14 ± 0.00	0.17 ± 0.01	3.594	0.001
i15:0	0.18 ± 0.00	0.26 ± 0.01	6.476	0.0001
a15:0	0.05 ± 0.00	0.07 ± 0.01	4.049	0.0001
4,8,12TMTD·	0.07 ± 0.00	0.10 ± 0.01	3.756	0.001
SAT total	(23.79 ± 0.17)	(27.52 ± 0.84)	-5.038	0.0001
14:1ω5	0.15 ± 0.05	0.19 ± 0.01		
16:1ω9	0.43 ± 0.03	0.41 ± 0.02		
16:1ω7	5.98 ± 0.10	6.67 ± 0.16	3.818	0.0001
16:1ω5	0.25 ± 0.00	0.33 ± 0.01	5.529	0.0001
17:1	0.40 ± 0.01	0.37 ± 0.01		
18:1ω9	29.79 ± 0.57	27.96 ± 0.77		
18:1ω7	5.12 ± 0.12	5.96 ± 0.11	4.895	0.0001
18:1ω5	0.58 ± 0.01	0.64 ± 0.02	3.677	0.001
20:1ω9	8.47 ± 0.23	9.60 ± 0.22	3.504	0.001
20:1ω7	0.50 ± 0.01	0.60 ± 0.02	5.269	0.0001
22:1ω11	1.21 ± 0.07	1.56 ± 0.12		
22:1ω9	0.92 ± 0.04	1.06 ± 0.05		
22:1ω7	0.11 ± 0.01	0.17 ± 0.01	4.048	0.0001
24:1	0.58 ± 0.01	0.84 ± 0.07		
MUFA Total	(54.92* ± 0.49)	(56.37 ± 0.92)		
C_{16}PUFA	0.28 ± 0.02	0.33 ± 0.01		
18:3ω6	0.07 ± 0.00	0.16 ±0.03	3.973	0.0001
18:4ω3	1.04 ± 0.05	0.85 ± 0.04		
18:2ω6	1.12 ± 0.07	1.00 ± 0.06		
20:4ω6	0.63 ± 0.02	0.50 ± 0.05		
20:3ω6	0.19 ± 0.00	0.17 ± 0.01		
20:4ω3	0.97 ± 0.03	1.20 ± 0.08		
20:5ω3	6.39 ± 0.17	4.67 ± 0.58		
20:2ω6	0.28 ± 0.01	0.29 ± 0.01		
22:5ω6	0.10 ± 0.00	0.06 ± 0.01	3.614	0.001
C_{21}PUFA	0.46 ± 0.02	0.35 ± 0.03	4.490	0.0001
22:6ω3	7.80 ± 0.34	4.97 ± 0.73	3.895	0.0001
22:5ω3	2.07 ± 0.07	1.57 ± 0.19		
PUFA Total	(21.37 ± 0.55)	(16.11 ± 1.52)	3.632	0.001
Σ ω3	(18.26 ± 0.56)	(13.25 ± 1.48)		
Σ ω6	(2.38 ± 0.08)	(2.18 ± 0.10)		
Ratio ω3:ω6	(7.92 ± 0.40)	(6.05 ± 0.63)	2.632	0.012

**includes minor proportions of other FA (16:1ω7t and 18:1ω7t)*

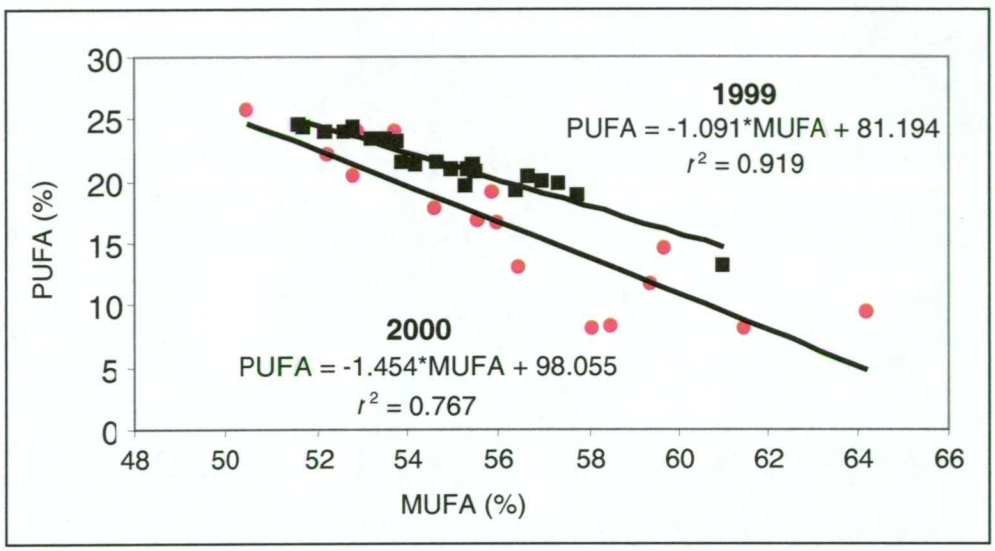


Figure 4.5 Relationship between monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) in 1999 and 2000 milk samples. Predictive equations for the proportion of polyunsaturated FA in milk samples are included in figure.

Table 4.6: Relationship between inter-annual differences in abundance of 9 fatty acids in fur seal milk samples and the occurrence of fatty acids in prey items.

Fatty acid	Year of highest abundance	Prey items
15:0	2000	Pt, Gp*, Es*
i15:0	2000	Gp*, Pt, Gf*, Es*
16:1ω5	2000	Gf*, Pt, Gp*
18:1ω7	2000	Gn*
20:1ω9	2000	Gn*, Mk, Ga
20:1ω7	2000	Ea, Ga, Gn*, Mk, Gf*
22:5ω6	1999	Mh
C_{21}PUFA	1999	Cg, Ga*
22:6ω3	1999	Mh, Tgaud*, Pt*, Cg

Mh *Martialia hyadesi*; Mk *Moroteuthis knipovitchi*; Ga *Gonatus antarcticus;* Cg: *Champsocephalus gunnari*; Ec *Electrona carlsbergi*; Es *E. subaspera*; Gf *Gymnoscopelus fraseri*; Gn *G. nicholsi*; Gp *G. piabilis*; Pt *Protomyctophum tensioni;* Tgaud *Themisto gaudichaudi.* *indicates higher incidence of prey item confirmed by scat analyses.

Of the three fatty acids occurring in higher proportions in milk samples in 1999, two: 22:5ω6 (DPA6) and 22:6ω3 (DHA), occurred in highest proportions in the ommastrephid squid *Martialia hyadesi*. Abundance of this species was much reduced in scats from 1999 (Table 4.2) however total frequency of occurrence of squid remains was similar between years at approximately 63%. Thus, the relatively high proportions of both these fatty acids in 1999 may indicate the presence of *M. hyadesi* in the diet over a longer time span than scat analysis is capable of detecting. However 22:6ω3 is also present in reasonable quantities in the amphipod *Themisto gaudichaudii* and *P. tenisoni*, both of which were more common in the diet in 1999 and are rich in PUFA.

4.4 Discussion

4.4.1 Limitations and assumptions of dietary techniques

There are many assumptions for all methods used to quantify the diet of a predator feeding at sea. Several studies have highlighted the errors associated with differential rates of digestion in relation to the hard parts of prey, particularly otoliths and squid beaks (Jobling and Breiby 1986; Pierce and Boyle 1991; Gales and Cheal 1992). Recent studies of sub-Antarctic fur seals (*A. tropicalis*) at Marion Island have found that scat analysis indicated a diet rich in myctophids (Klages and Bester 1998) whilst analyses of stomach contents for the same species at Marion (Ferreira and Bester 1999) and Gough Islands (Bester and Laycock 1985) revealed a predominance of squid in the diet. Unfortunately it is very difficult to account for many of these problems when studying free-ranging animals without the lethal take of individuals, and ideally studies of passage rates would be conducted simultaneously (see Staniland 2002). However, given that our primary aims were to identify any shifts in diet over several years, many of the elements that make dietary quantification difficult, such as biases associated with the passage rates of various prey items, should remain relatively constant when similar techniques are used between years, thereby enabling a comparative study such ours to draw conclusions about relative change with some confidence. By utilising two techniques of dietary assessment we have shown that whilst female Antarctic

fur seals prey primarily on myctophids at Cap Noir, Îles Kerguelen, species composition of their diet varies significantly between years most probably in response to changes in prey availability affected by inter-annual shifts in the positioning of oceanic frontal structures and associated marine productivity (see Guinet *et al.* 2001).

4.4.2 Diet composition

The importance of fish, particularly myctophids, as the main prey items of Antarctic fur seals at the Kerguelen Archipelago was confirmed by faecal analyses and support the previous findings of Cherel *et al.* (1997) and Guinet *et al.* (2001). Myctophids inhabiting the Antarctic Polar Frontal Zone (Duhamel *et al.* 2000), dominated the diet in February in all three years, both by number and reconstituted mass. *Gymnoscopelus piabilis* was consistently the most common species present in the diet. This species is also present in the diet of conspecifics at Macquarie Island and Marion Island (Goldsworthy *et al.* 1997; Klages and Bester 1998; Robinson *et al.* In Press) and King penguins at the Crozet Archipelago (Cherel *et al.* 1996) and has even been reported in the diet of New Zealand fur seals in the temperate waters of southern Tasmania (Lake 1997). In addition to *G. piabilis*, *E. subaspera* and *G. nicholsi* were consistently important in the diet. These species are mesopelagic/epibenthic (Hulley 1990) and are present in the upper part of the mesopelagic fish community of the PFZ, being absent in daytime trawls at 300m and abundant at the surface at night (Duhamel *et al.* 2000). The behaviour of female Antarctic fur seals foraging nearby Îles Kerguelen, is apparently determined by the diurnal movements of their prey. Antarctic fur seals typically dive nocturnally, commencing at considerable depth, with dives generally becoming progressively shallower throughout the night in conjunction what is assumed to be the simultaneous migration of prey (Chapter 2).

Gymnoscopelus piabilis is large in size in comparison to other myctophids and high in calorific value (Raclot *et al.* 1998) and may therefore be an advantageous species in terms of efficient energy consumption during lactation for Antarctic fur seals. The diet of Antarctic fur seals from Ile de Croy to the Northwest of the archipelago in late lactation 1994 was also dominated by a *Gymnoscopelus* species, *G. nicholsi* (Cherel *et al.* 1997), a species often associated with the continental slope (Daneri 1996). This species is capable of forming dense concentrations (Kozlov 1995), and is one of the four most abundant myctophids in the Southern Ocean, the other three being *Electrona antarctica*, *E. carlsbergi* and *Krefftichthys anderssoni* (Kozlov and Tarverdiyeva 1989). *Gymnoscopelus nicholsi* is also particularly oily (Chapter 3), although smaller in size than *G. piabilis*, and comprised a significant portion of the diet of seals from Cap Noir, particularly in 2000. Apart from *G. piabilis*, *G. fraseri* and some *E. antarctica* and *P. tenisoni* in 2000, virtually all myctophids in the diet of Antarctic fur seals had not yet attained maturity (Hulley 1990).

While myctophids of the PFZ generally constituted the major dietary components of the fur seals, differences at the species level were evident between years, and in 1998 in particular the consumption of other fish species represented 36% of prey biomass. The most common of these species (17%), the mackerel icefish (*Champsocephalus gunnari*) is also trawled commercially at Îles Kerguelen (Duhamel 1991). This species usually occurs over shelf/upper slope waters over depths of 150-300m during the day, becoming more pelagic at night (Duhamel 1991). *Champsocephalus gunnari* is known to forage on many of the smaller myctophid species also present in the scats of A. *gazella*, such as *K. anderssoni, Metelectrona ventralis, Protomyctophum andriashevi and P. choriodon* (Hulley 1990), some of which may be secondarily ingested from the stomachs of *C. gunnari* in 1998. The diet of *C. gunnari* at Kerguelen is however, usually comprised of the amphipod *Themisto gaudichaudii* and the euphausiid *Euphausia vallentini* (Duhamel and Hureau 1985) perhaps explaining the higher incidence of these species in scats in 1998. *Themisto gaudichaudii* is especially abundant in Kerguelen waters where it plays a major trophic role in the pelagic ecosystem (Bocher *et al.* 2001). Icefish consumed by fur seals in 1998 were from the cohort age 1+, and averaged 193mm in length representing the largest of the fish species consumed in high numbers. It is possible that the heads of larger fish were not consumed, as is frequently the case with Cape fur seals (*A. pusillus pusillus*; David 1987) and were thus not represented in scats. Icefish is not particularly high in calories at 5.4 kJg^{-1} (Chapter 3) when compared to myctophids such as *G. piabilis* or *G. nicholsi* (9.5-9.8 kJg^{-1}), however one icefish is equivalent in calorific value to several smaller and oilier myctophids, as a result of their larger size. Commercial trawlers conducting research trawls in the vicinity caught only larger, older fish of age 3+ measuring 310mm (Claudet 2001). Thus it would appear that seals and trawl gear are capturing different sized fish.

At other Antarctic fur seal breeding sites such as Bird Island, South Georgia, and Heard Island, *C. gunnari* is usually found in the diet of male fur seals (North *et al.* 1983; Reid 1995; North 1996; Green *et al.* 1997), although it is also a relatively important dietary component of female fur seals in years of low krill abundance around Bird Island (Reid and Arnould 1996). North (1996) observed two size classes of *C. gunnari* in the diet of fur seals over winter with the majority of those taken coinciding with the size classes trawled by the fishery (225-325mm). At Heard Island two peaks were detected at 195 and 225mm in winter and summer respectively (Green *et al.* 1997), coinciding with the size of fish taken by seals at Îles Kerguelen in 1998. *Champsocephalus gunnari* was not present in the diet in either 1999 or 2000 at Îles Kerguelen, although research trawls caught low numbers of 244 mm and 313 mm sized fish in the two years respectively (Claudet 2001). The consumption of

Icefish in 1998 may reflect either the reduced availability and/or catchability of myctophids close to the archipelago in this year, or more patchily distributed icefish in 1999 and 2000.

Cephalopod beaks were common in seal scats, although they occurred in low numbers when compared to the quantities fish prey consumed, accounting for only 2.1% of prey by number. At least four of the squid species taken by Antarctic fur seals are associated with waters of the PFZ and are known to feed on myctophids (Rodhouse and White 1995; Gonzàlez and Rodhouse 1998; Phillips *et al.* 2001). Only juvenile *M. hyadesi*, *M. ingens* and *M. knipovitchi* (Kubodera *et al.* 1998; Wormuth 1998) were taken by seals foraging in the Kerguelen region. Given the low numbers of squid present in the diet it is probable that squid were either taken opportunistically as seals and squid fed on nocturnal myctophid aggregations, or the squid were patchier in their distribution than myctophids. Studies of Antarctic fur seals at other breeding sites confirm the relative paucity of cephalopods in the diet (Klages 1996; Goldsworthy *et al.* 1997; Daneri *et al.* 1999), contrary to studies of more generalist, temperate species such as the New Zealand and Australian fur seals (Gales *et al.* 1993; Fea and Harcourt 1997; Harcourt *et al.* 2001), and female southern sea lions at the Falkland Islands, which also prey heavily on *M. hyadesi* in some years (Thompson *et al.* 1998). In any event, the occurrence of cephalopods in the diet of Antarctic fur seals was low and never accounted for more than 2.1% of the diet by number, a figure that would be over-estimated by the preferential retention of squid beaks (see Klages and Bester 1998; Ferreira and Bester 1999). However in years where squid were consumed, such as 1998 and 2000, the biomass and energy value of this prey was considerable ranging from 10-15% of reconstituted biomass.

4.4.3 Milk lipids as indicators of dietary variation

The dietary dependence of fur seals on myctophids during late lactation was further confirmed by the high levels of MUFAs present in the fatty acid profiles of fur seal milk. Myctophidae generally have high levels of MUFAs (Seo *et al.* 1996; Raclot *et al.* 1998), which may be transferred directly to predators, as shown by the close relationship between the fatty acids of king penguin subdermal fat and of their myctophid diet (Raclot *et al.* 1998). The percentage of MUFAs in fur seal milk (53-55%) more closely approximates that of triacylglycerol-rich myctophids rather than those species rich in wax esters, such as *Electrona antarctica* or *Gymnoscopelus braueri* (Phleger *et al.* 1999) thus confirming the findings of the faecal analyses. High levels of 18:1ω9, 20:1ω9, and 22:1ω11, apparent in fur seal milk samples, also tend to be characteristic of many teleost fish (Reinhardt and van Vleet 1986; Iverson *et al.* 1997a).

Milk secreted later in lactation is thought to contain fatty acids representative of dietary intake, whilst fatty acids present in blubber stores during the peri-natal period may represent dietary intake over winter prior to parturition (Iverson 1993; Iverson *et al.* 1997a). Mammalian milk composition varies according to lactation stage (Oftedal 1984). Consequently, milk samples for this study were collected at the same season in both years, in order to reduce the effect of any compositional differences related to lactation stage or season. Thus, the differences observed in the fatty acid composition of milk samples in two consecutive years in this study confirm the inter-annual shift in diet detected by faecal analysis.

The similarity of milk samples from the same seal collected up to 19 days apart suggests that seals may feed on similar prey during successive trips, therefore exhibiting little change in their milk fatty acid profiles; or that milk fatty acids may be indicative of dietary intake over at least 19 days and fatty acid profiles are therefore not particularly responsive to short-term changes in prey consumption. Little information is available on short-term dietary preferences, although (Bonadonna *et al.* 2001) have recently shown that fur seals at Cap Noir often maintain the direction of travel used in the preceding trip, perhaps foraging on the same prey. However, in either scenario it is probable that milk fatty acid compositional profiles represent longer-term dietary intake, at least up to three weeks, than faecal analyses.

Milk samples collected during late lactation 1999 were high in PUFAs (21.4% *cf.* 16.1%) whilst samples from 2000 where higher in saturated and monounsaturated fatty acids. Nine fatty acids were identified by DFA as differentiating between milk samples from the two years. Of these fatty acids, 18:1ω7, indicative of *G. nicholsi* consumption, was particularly useful in confirming the higher incidence of this species as shown by scat analyses. Also the higher levels of PUFAs in 1999, DHA (22:6ω3) in particular, could indicate a greater reliance on *Protomyctophum tenisoni,* which are relatively high in DHA (Chapter 3), than detected by faecal analyses because of their small, digestible otoliths.

The significance of such comparisons is undoubtedly influenced by both the number, and site of origin of potential prey items. Fish of the same species from different localities may vary considerably in FA composition. Fortunately we could compare milk samples with fatty acid profiles of 8 prey species collected in the foraging zone of fur seals (see Chapter 3). However, the fatty acid profiles of many prey species, in particular *Protomyctophum* spp., are yet to be described at Îles Kerguelen, and in many regions of the Southern Ocean.

Previously, significant seasonal shifts in dietary intake of Antarctic fur seals at South Georgia have been identified by Iverson *et al.* (1997a) using fatty acid signature analysis,

whilst Brown *et al.* (1999) could distinguish between the diet of Antarctic fur seals and Southern elephant seals from South Georgia by comparing the fatty acid composition of milk samples to potential prey items. More recently, grey seals from different breeding sites have been differentiated on the basis of milk fatty acid profiles alone without reference to possible prey items (Walton *et al.* 2000). Thus the usefulness of quantitative FA analysis in answering particular questions regarding prey group consumption or inter-site dietary differences is beyond doubt. Although it was possible to statistically discern between milk samples from two consecutive years on the basis of milk FA profiles at Îles Kerguelen, isolating those species attributing to the observed difference was less clear. Considerable debate regarding the statistical analysis and interpretation of dietary signature FA analysis has taken place in recent years and although this study provides support for the occurrence of dietary shifts using milk FA analysis, further developments in the analytical tools used to adequately interpret such data are still necessary.

Approximately 94% of the Antarctic fur seal diet (according to scat analysis) at Îles Kerguelen consists of myctophid fish. The variation in FA composition recorded between species of myctophids is minimal when compared to the larger scale differences between fish, prey items of other trophic levels and milk profiles. Had milk samples been collected in 1998, a year of higher consumption of fish from other families, such as *C. gunnari*, differences in milk compositional profiles may have been more easily attributed to particular prey family or species.

Interestingly, the proportion of lipid in milk samples also differed between years in addition to the fatty acid profile differences. Percentage lipid was particularly high in 2000 samples (53%), which were still within the range of values reported by Arnould and Boyd (1995) for conspecifics in late lactation at South Georgia, and Robinson (In Press) at Macquarie Island. Myctophids of the Genus *Gymnoscopelus* and *Electrona antarctica* are particularly rich in lipid with up to 18% lipid g^{-1} wet mass reported for *G. nicholsi* from the Kerguelen region (Chapter 3). One hypothesis for the observed inter-annual variation in milk lipid content in 1999 and 2000 is the variability in the consumption of *Gymnoscopelus* spp. in the two seasons, which comprised approximately 54% of the dietary biomass in 1999 and 74% in 2000 (or 57% and 80% in terms of energy respectively), perhaps explaining, in part, the inter-annual variation in milk lipid content. Thus it would appear that differences in diet between years might also affect the quality of milk stores delivered to pups.

4.4.4 Implications for foraging ecology and oceanic conditions

On a broad taxonomic scale, the composition of the diet between years was similar as myctophids consistently formed the majority of the diet both by number and in terms of

biomass. In all years *Gymnoscopelus piabilis* comprised between 27-32% of prey biomass. However, on a finer scale the composition of prey species was highly variable with the occurrence of icefish (*C. gunnari*), and *E. carlsbergi* in 1998, a greater proportion of *Protomyctophum* species in 1999, and perhaps squid, and a considerably higher proportion of *G. nicholsi* and myctophids in general, in 2000. Changes in oceanographic circulation appear to be responsible for fluctuations in prey abundance (Hunt 1991; McCafferty *et al.* 1999; Nel *et al.* 2001) and the position of oceanographic features, such as the PF may be affected seasonally by weather systems (Priddle *et al.* 1988). Reid and Arnould (1996) have suggested that periods of myctophid consumption by female Antarctic fur seals at South Georgia, which usually feed on Antarctic krill, coincide with oceanographic changes bringing concentrations of myctophids, associated with the PF, into the foraging range of the seals. Thus it is reasonable to suggest that the position of the PF and oceanographic conditions at Kerguelen varied sufficiently within the foraging range of fur seals from 1998 to 2000 to change the species composition of prey available to fur seals.

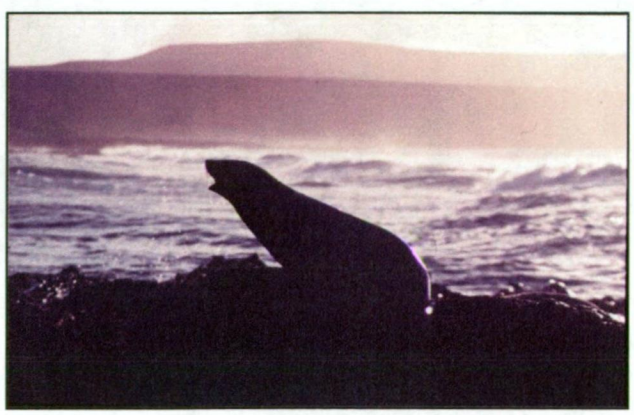
Guinet *et al.* (2001) have recently demonstrated that in February 1998 female Antarctic fur seals at Îles Kerguelen tended to forage in the vicinity of the Polar Front in areas of high fish abundance over the continental slope. In our study, 1998 was the year of least myctophid abundance in the diet in comparison to the other two years, and was also the year that seals dived most deeply on average (Chapter 2). Thus it would appear that prey availability as measured by the diving behaviour of the seals (Boyd 1999), and confirmed by dietary analysis, varied considerably between years. The higher incidence of scats devoid of otoliths and prey remains in 2000 also tends to suggest that seals were foraging further from the colony in this year. All these factors indicate that possible changes in oceanographic features in the vicinity of the Kerguelen Archipelago from 1998-2000 affected the dietary intake and foraging behaviour of Antarctic fur seals considerably.

4.5 SUMMARY

- dietary preferences of female Antarctic fur seals from Cap Noir foraging in the PFZ were studied in February of 1998, 1999 and 2000
- scats were collected and analysed for remaining hard-parts in each of the three years, and in 1999 and 2000 the fatty acid composition of fur seal milk samples was also examined for longer term dietary preferences
- scat analysis indicated a primarily fish diet with the inclusion of some squid in all three years (25 species of fish being taken during the study)
- myctophids accounted for an average of 94% by number of all fish consumed with three species, *Gymnoscopelus nicholsi*, *G. piabilis* and *Electrona subaspera*, forming the core diet
- inter-annual differences in dietary species composition were apparent with the presence of mackerel icefish *Champsocephalus gunnari,* and the myctophid *Protomyctophum tenisoni* accounting for the differences observed between years in 1998 and 1999, respectively.
- reconstituted prey biomass per scat was similar between years, although scats from 1998 represented less energy per gram than those from 1999 and 2000
- the study highlighted the usefulness of using FA signature analysis to confirm longer term shifts in dietary intake of fur seals using milk samples
- PUFAs were significantly more prevalent in the 1999 milk samples, which were also lower in overall lipid content (43% *cf.* 53%)
- *Gymnoscopelus nicholsi,* a particularly oily fish, occurred in higher proportions in the diet in 2000, perhaps explaining the higher incidence of MUFAs in this year and the generally higher lipid levels present in milk samples
- inter-annual variation in diet of Antarctic fur seals was confirmed by two independent techniques
- findings support the hypothesis that previously identified variation in oceanographic conditions surrounding Îles Kerguelen in 1998, 1999 and 2000 affect the availability of fur seal prey resources.

Chapter 5

Fine scale foraging behaviour of Antarctic fur seals in relation to environmental conditions



5.1 Introduction

Oceanic environments are often patchy in their distribution of resources, there being many processes determining the distribution of nutrients and subsequent productivity. In the Southern Ocean (SO), phytoplankton blooms are often associated with coastal/shelf waters, sea-ice retreat and major fronts (Moore and Abbott 2000). In the Antarctic Polar Frontal Zone (PFZ), and the SO generally, waters are high in nutrients and low in chlorophyll (HNLC; Abbott *et al.* 2000). In the PFZ, spring blooms of phytoplankton, which are a feeding source for many species of zooplankton, are initially limited by light levels associated with deep, late spring mixing of the water column (Abbott *et al.* 2000). Sea surface temperatures (SST) are also an important component in models estimating local maximum rates of primary production (Behrenfeld and Falkowski 1997; Moore and Abbott 2000). As the austral summer progresses and water column stratification occurs, grazing by zooplankton, and levels of iron (de Baar *et al.* 1995; Trull *et al.* 2001) and silica (Prego *et al.* 1999) will control the maximum chlorophyll concentration (Abbott *et al.* 2000). Such variability in marine productivity is likely to be passed down the food chain to higher trophic levels, firstly to zooplankton and their immediate consumers such as mesopelagic fish and squid, and eventually to top-level predators.

Zooplankton such as krill (*Euphausia superba*) and other crustaceans form the dietary basis of many SO seabirds and penguins (Hull 1999; Bocher *et al.* 2000; Bocher *et al.* 2001) and their abundance at the meso-scale is generally related to hydrographic features such as the position of fronts and eddies (Pakhomov and McQuaid 1996; Ansorge *et al.* 1999; Pakhomov and Froneman 2000). The distribution of pelagic fish and squid (Duhamel *et al.* 2000), which themselves are preyed upon by top-level predators, is determined by the concentrations and migrations of macrozooplankton in the water column (Froneman *et al.* 2000; Reid and Hindell 2000). Thus the influence of hydrographic features on the foraging distribution of higher order predators may be considerable. Black-browed albatross (*Diomedea melanophris*) breeding on the Kerguelen Archipelago are found in high concentrations over the continental shelf break, a region of increased productivity levels (Cherel *et al.* 2000). Nel *et al.* (2001) have also recently linked the foraging behaviour of grey-headed albatross (*Thalassarche chrysostoma*) to the occurrence of sea surface height (SSH) anomalies representing eddies, in the vicinity of the Prince Edward Islands. Furthermore, King penguins (*Aptenodytes patagonicus*) at the Crozet Archipelago typically forage at the PF in summer (Guinet *et al.* 1997; Koudil *et al.* 2000) and in Antarctic waters in autumn and winter (Charrassin and Bost 2001).

The foraging success, and subsequent breeding success, of marine predators such as seabirds, seals and penguins is ultimately determined by the spatial and temporal occurrence of regions of oceanic productivity (see Schneider 1990; Hunt 1991; Guinet *et al.* 2001) and the ability of predators to locate and effectively exploit these patchily distributed resources. Relationships

between the concentration of prey and the distribution of their predators are often scale-dependent. At large scales, aggregations of seabirds at sea may be indicative of high prey biomass below birds (Mehlum *et al.* 1996; Swartzman and Hunt 2000) while at small scales (10s of km) seabirds may appear to select for frontal zones (Hunt 1991; Mehlum *et al.* 1998), which are often thought to represent regions of enhanced biological activity (Lutjeharms *et al.* 1985). A recent study comparing aggregations of seabirds (murres) to capelin abundance at large (200-300km) and small (70km) spatial scales found that at the large scale, correlations between the two species increased with increasing capelin density and patchiness (Fauchald and Erikstad 2002). While at the small scale, concordance increased only with increasing capelin patchiness. Thus the scale at which relationships between predators and prey are studied may greatly affect the outcome (Wiens 1989).

Finding a relationship between the spatial distribution of marine mammals, their prey and oceanographic features has proven more challenging, largely because of the reduced likelihood of sightings of underwater predators. Associations between the distribution of whales and oceanographic features (Tynan 1997) and chlorophyll concentrations (Jaquet and Whitehead 1996; Jaquet *et al.* 1996) have been reported on relatively large scales using whaling data. While other studies have identified relationships between the at-sea distribution of seals and frontal water masses using data-loggers (Hindell *et al.* 1991; Boyd *et al.* 2001; Field *et al.* 2001; Bradshaw *et al.* 2002). Few studies, however, have been successful at identifying predator-prey relationships of marine mammals on smaller scales (<1.0° latitude).

One species for which relationships between distribution, foraging activity and marine productivity at relatively small scales have been observed is the Antarctic fur seals (*Arctocephalus gazella*). This species exhibits flexible foraging behaviour, feeding on a mixture of krill or mesopelagic fish and squid at their various breeding sites (Reid and Arnould 1996; Cherel *et al.* 1997; Goldsworthy *et al.* 1997; Green *et al.* 1997; Klages and Bester 1998). Females, constrained by their brief lactation period (Boyd and McCann 1989) must find reliable prey resources from December to April each year in the vicinity of their colony. As central place foragers (Orians and Pearson 1979), the fur seals are limited in their ability to explore the marine environment in search of prey, and by the fasting capabilities of and growth requirements of their pup (Guinet *et al.* 2001). Many sequential years of research at South Georgia have indicated that in years where prey availability is diminished around the island, reproductive success is reduced and catastrophic breeding failures may occur (Boyd *et al.* 1995).

The Kerguelen Archipelago, a summer breeding site for Antarctic fur seals, is located in a region of hydrographic complexity (Belkin and Gordon 1996), bounded to the south by the Polar Front. Myctophid fish, the preferred, energy-rich prey of Antarctic fur seals in this region

(Cherel *et al.* 1997; Chapter 4), occur in high densities within the PFZ to the north and east of the Archipelago (Duhamel *et al.* 2000). Fur seals typically prey on nocturnally surface migrating myctophids, spending up to 70% of their time at night diving (Chapter 2). However, a high level of variability exists in several aspects of foraging between individual seals from the same colony, both in terms of their dive behaviour (Chapter 2), and in the direction of travel taken from the colony (Bonadonna *et al.* 2001). Guinet *et al.* (2001) have further demonstrated that in 1998 the diving activity of seals, in terms of time spent diving per sector, was related to oceanographic conditions, forage fish distribution and distance from the colony at varying spatial scales (0.1-3.0° latitude). Significant relationships were found at the population level between time spent diving by seals in a particular region and distance from the colony, bathymetry and chlorophyll levels (Guinet *et al.* 2001). For the majority of these parameters the strength of the correlation decreased with increasing scale suggesting that fur seals were responding to small-scale changes in these features. The one exception to this, was the association between diving activity and chlorophyll concentrations, which was negatively related to near-surface chlorophyll concentration at a small spatial scale but was positively related at medium scales (1.0°; Guinet *et al.* 2001).

In this paper we were interested to investigate whether female Antarctic fur seals change their level of diving activity on a nightly basis in relation to environmental characteristics (Chlorophyll-*a* concentration, sea surface temperatures and bathymetry) encountered within their foraging areas. We examine fine scale relationships (0.1°-1.0° latitude) between diving activity, as measured by 7 diving parameters, and the environmental conditions. Given the high degree of variability previously noted in individual diving behaviour between sites and years (Chapter 2) we hypothesise that localised changes in oceanographic conditions could determine some of this variability. Even on a small scale, differences in levels of energy transfer from mother to pup may also be anticipated under variable environmental conditions. Thus a secondary aim of the study is to investigate the relationship between the provisioning of young, maternal diving activity and variation in oceanographic parameters.

5.2 Materials and methods

Antarctic fur seals breed at several sites along the north and east coasts of the Kerguelen Archipelago in the southern Indian Ocean. Seals were studied at a breeding colony at Cap Noir (49°07'S, 70°45'E) on the north-east coast of the Courbet Peninsula where approximately 800 females breed annually. Seals arrive at the colony in November and December each year and give birth to a single pup, which they then suckle for approximately 4 months. Female seals at the Kerguelen Archipelago forage at sea for 2.7 to 17.9 days (Chapter 2&6; Guinet *et al.* 2001), returning to suckle their pups for periods of approximately 2 days.

5.2.1 Oceanographic environment

In the Kerguelen region, the Antarctic Polar Front (PF) is defined as the northern terminus of the 2.5°C isotherm in the 100-300m layer of the water column (Belkin and Gordon 1996). The PF generally passes south of the Kerguelen Archipelago (Park *et al.* 1991; Sparrow and Heywood 1996) but occasionally moves north of the islands (Moore *et al.* 1999a). Bottom topography of the Kerguelen Plateau exerts strong topographic control in this region (Gambéroni *et al.* 1982; Sparrow and Heywood 1996) forcing branches of the Antarctic Circumpolar Current (ACC, Orsi *et al.* 1995) to within 2-3° of latitude to the north of the Archipelago (Park *et al.* 1991). The ACC comprises three fronts at this location (47-49°S, 65-75°E): (1) the Sub-tropical Front (STF); (2) the Sub-Antarctic Front (SAF) and (3) the PF. The STF to the north and the PF to the south bound the Polar Frontal Zone (PFZ, Klyausov 1990; Belkin and Gordon 1996), which encompasses the Kerguelen Archipelago. The PFZ to the east and downstream of the archipelago is an area of elevated nutrients (Prego *et al.* 1999; Bucciarelli *et al.* 2001), high primary productivity (Moore *et al.* 1999b; Moore and Abbott 2000; Blain *et al.* 2001), abundant zooplankton (Pakhomov 1997), and fish (Duhamel *et al.* 2000).

5.2.2 At-sea distribution of seals

Seals were caught in the colony using a hoop net, and were held for up to 20 minutes on a restraint board whilst devices mounted on nylon webbing with cable ties were attached dorsally between the scapulae with two-part epoxy adhesive (AW2101; Ciba Specialty Chemicals Holding Inc. Switzerland). In February 2000, ten female seals were equipped with ARGOS satellite platform terminal transmitters (PTTs, ST-10 electronics, Telonics AZ, USA potted by Sirtrack, New Zealand, 110x42x14 mm). Locations of seals at sea were obtained via the ARGOS satellite system (Taillade 1993). A Mk7 Time-Depth Recorder (TDRs, Wildlife Computers, Redmond, 100x20x10 mm, 30g) was attached dorsally to each PTT to enable the diving behaviour of seals to be associated with the seal's position at sea. The combined PTT/TDR packages (110x42x25mm, 150g, Bonadonna *et al.* 2001) were hydro-dynamically shaped with nautical putty to reduce drag.

Seals, and their pups, were weighed, measured and given a unique identifying mark on the rump with Clairol hair dye (Born Blonde, Bristol Myers Squibb, NSW, Australia). Pups were also weighed daily during their mother's absence with a Salter Weightronix spring balance (25±0.02 kg) to obtain an accurate estimate of mass gain by the pup (PMG) once the mother had returned (see Guinet *et al.* 1999 & 2000). The body mass gain of the pup is expressed in absolute terms as the quantity of mass gained while the mother was ashore (absolute PMG) and as daily PMG per foraging cycle (FC; shore bout and foraging trips in days; Guinet *et al.* 1999; Guinet and Georges 2000), which can be used as a comparative measure of foraging efficiency.

Only ARGOS class 3, 2, 1 and 0 locations were used in analyses. Data were filtered such that locations requiring a transit speed greater than 3 $m.s^{-1}$ were discarded. This speed had previously been determined for seals carrying velocity TDRs (Wildlife Computers) as the highest speed generally attained by fur seals from Cap Noir (see Bonadonna *et al.* 2001). As the majority (87%) of foraging activity by females occurs at night (Chapter 2) only nocturnal locations were regarded as identifying foraging zones. A mean nightly position was calculated for each seal if more than one location was available. Positional data for a total of 35 foraging nights were available after the removal of incomplete nights due to time spent by seals in transit to foraging areas. Distances from the colony (km) were also calculated for each nocturnal foraging location using the great circle distance formula (Donnay 1997).

5.2.3 Diving behaviour

Dive data were extracted using Wildlife Computers software and the offset and drift of pressure transducers were corrected using customised software (Chapter 2). All TDRs were programmed to record depth (±1m) and temperature (±0.1°C) every 5s. Each TDR was calibrated in a thermostatically controlled bath after the study. All units reliably recorded temperatures of 0-10°C to within 0.1°C, therefore we have used manufacturers temperature calibrations. SST data (depth <4m) were also extracted from TDR records between the hours of 2300 and 0100 hrs (Georges *et al.* 2000b) to examine temporal changes in SST throughout the duration of a foraging trip. By sampling only at night, potential increases in temperature associated with solar radiation are avoided, however some degree of thermal lag is anticipated due to the change in temperature associated with depth (Charrassin and Bost 2001; Field *et al.* 2001). McCafferty *et al.* (1999) noted a lag of <10s for dives of <60m (mean=3.9s) during TDR deployments on Antarctic fur seals at South Georgia, although lag times of dives >60s exceeded 20s. Thus a slight lag in the response time of deeper diving seals at Kerguelen may be anticipated. The duration of day and night periods were calculated using sunrise and sunset times at Cap Noir estimated by AUSLIG software (Department of Industry Science and Resources, Canberra, Australia). The duration of night ranged from 9.0 to 10.6 hours during the course of the study.

In Chapter 2, the diving behaviour of fur seals at Îles Kerguelen over three years was examined using 12 dive parameters per foraging trip. For this study we have modified the number of parameters, selecting only those parameters applicable to an individual night of foraging effort, rather than an entire trip. These parameters were: (1) dive frequency (number of dives per hour of night); (2) mean dive depth (m); (3) mean dive duration (s); (4) vertical depth (km) dived per hour of night (cumulative dive depth x 2 per hour of night); (5) mean number of dives per bout; (6) proportion of all dives in bouts (%); and (7) time spent diving (%).

5.2.4 Environmental data

Bathymetric data at each foraging location were extracted from the ETOPO5 database (5' x 5' resolution). The Multi-Channel Sea Surface Temperature (MCSST) data were derived from the 5-channel Advanced Very High Resolution Radiometers (AVHRR) on board the NOAA –7, -9, -11 and –14 polar orbiting satellites. The MCSST (°C) for February 2000 were obtained from the PODAAC (Physical Oceanography Distributed Active Archive Center) by file transfer protocol (ftp) on *ftp://podaac.jpl.nasa.gov/pub/sea_surface_ temper ature/avhrr/mcsst/*. Weekly average data for the descending path were used on an equal-angle grid of 2048 pixels longitude by 1024 pixels latitude (nominally referred to as the 18km resolution). Surface chlorophyll-a concentrations were obtained from global and regional ocean colour data obtained by the Sea-viewing Wide field-of-view Sensor (SeaWIFS), in orbit on the OrbView-2 (formerly Seastar) platform. We used the SeaWIFS Level 3 monthly product containing monthly data that have been "binned" and spatially/temporally averaged into 9km grid cells encompassing the globe. Because of the high level of cloud coverage in the Kerguelen region, the 8-day data are insufficient, requiring the use of monthly record of surface chlorophyll-a concentration (mg m^{-3}) for February 2002.

To link diving behaviour and environmental parameters we extracted the environmental data in the area corresponding to the dive locations. To evaluate the effects of the spatial range on our analysis we calculated the mean for MCSST within an area of changing radius around the nocturnal diving location. Weekly MCSST data were extracted at the following three spatial scales: directly under the location of nocturnal diving activity (0.1°x0.1°), and within a circle with radii of 0.5° and 1.0° surrounding this location.

5.2.5 Software

Raw data were extracted using SeaDas software (SeaWIFs Data Analysis System, see SeaDas Home Page: http://seadas.gsfc.nasa.gov/). All data extraction under and around the area of diving activity was done using ArcView GIS and Spatial Analyst Extension (ESRI).

5.2.6 Statistical analysis

Clustering and multidimensional scaling of environmental and physical parameters (MCSST, Chlorophyll-*a* concentration and bathymetry) at 35 nocturnal foraging locations were conducted at each of the three spatial scales (0.1°, 0.5° and 1.0° radii) to identify possible environmental groupings (ecoregions, see Hargrove and Hoffman 1999). This objective method of classification was chosen particularly in response to the uneven number of foraging nights per seal (1-7) present within the data set. Although this represents a lack of independence in the data, interpretation of the links between fine scale foraging activity (diving parameters) and environmental variables will be discussed on a per seal basis. A clustering algorithm (UPGMA;

Belbin *et al.* 1992) and non-hierarchical agglomerative fusion strategy (see Chapter 2) were then used, producing a dendrogram at each spatial scale. The number of potential ecoregions was selected objectively by forcing the data into 2, 3, 4, 5 and 6 ecoregions. The physical characteristics were then ordinated in 3-dimensions by MDS. Foraging nights were assigned to an ecoregion at each of the three spatial scales based on the cluster analysis. Two to six ecoregions were identified at each spatial scale.

The seven dive parameters at each of the 35 foraging locations were then included in a backwards stepwise discriminant function analysis (DFA) to ascertain firstly, how many ecoregions could be reliably distinguished by the diving activity of seals and secondly, at which spatial scale the relationship was most accurate. Those diving parameters most influential in distinguishing between ecoregions were also identified by the backwards DFA. Any univariate statistics such as regression analysis were conducted using only mean values per seal, which are reported ± standard error of the mean (SEM).

5.3 Results

5.3.1 At-sea distribution of seals

Of the 35 foraging nights for which at-sea locations were recorded for the 10 seals, only 4 of the nights occurred over the continental waters of the Kerguelen Plateau (<500m). Thirteen nights were located over the continental shelf break (500-1000m) and 18 were located over pelagic waters (>1000m). The foraging locations of the seals were relatively dispersed with seals either travelling to the north-east or south-east of the colony (Fig. 5.1). Generally, seals dispersed in an arc from the north-east through to the south-east, usually within 230.6±36.8 km of the colony (n=9). One seal (H3) travelled to a region 448 km east of Cap Noir in a foraging trip lasting 12.3 days (Table 5.1). The mean foraging distance from the colony for the 35 nights was 155.1±31.7km (22.0-312.6km).

Table 5.1: Deployment history, pup mass gain & maximum distance travelled from the colony for *Arctocephlaus gazella* females in February 2000.

Seal	Departure date	Trip length (d)	No. of nights	Mean maternal mass (kg)	Maximum distance (km)	Direction of travel	Pup sex	Pup mass gain (PMG kg)	Daily PMG (kg d^{-1})**
H3	29.1.00	12.3	7	34.8	448	NE*	F	3.84	0.242
H4	30.1.00	8.9	5	29.4	193	NE	M	2.47	0.225
H5	30.1.00	6.2	1	29.7	186	SE	F	2.01	0.255
H6	31.1.00	9.3	4	33.9	259	SE	M	2.94	0.241
H7	29.1.00	8.8	3	28.3	251	SE	F	2.62	0.237
H8	31.1.00	5.2	2	31.5	114	NE	M	2.06	0.294
S1	12.2.00	9.1	4	33.6	215	SE	M	.	.
S2	17.2.00	4.0	2	31.7	.	NE	F	0.65	0.109
S3	18.2.00	6.0	3	31.1	81	NE	F	1.38	0.175
S4	24.2.00	10.4	4	33.1	328	SE	F	3.78	0.298
Mean		8.0± 0.8	3.5	31.7± 0.7	231± 37			2.41± 0.35	0.231± 0.019

* colony-preferred direction (see Bonadonna *et al.* 2001); ** per foraging cycle (FT + SB; Guinet *et al.* 1999; Guinet and Georges 2000)

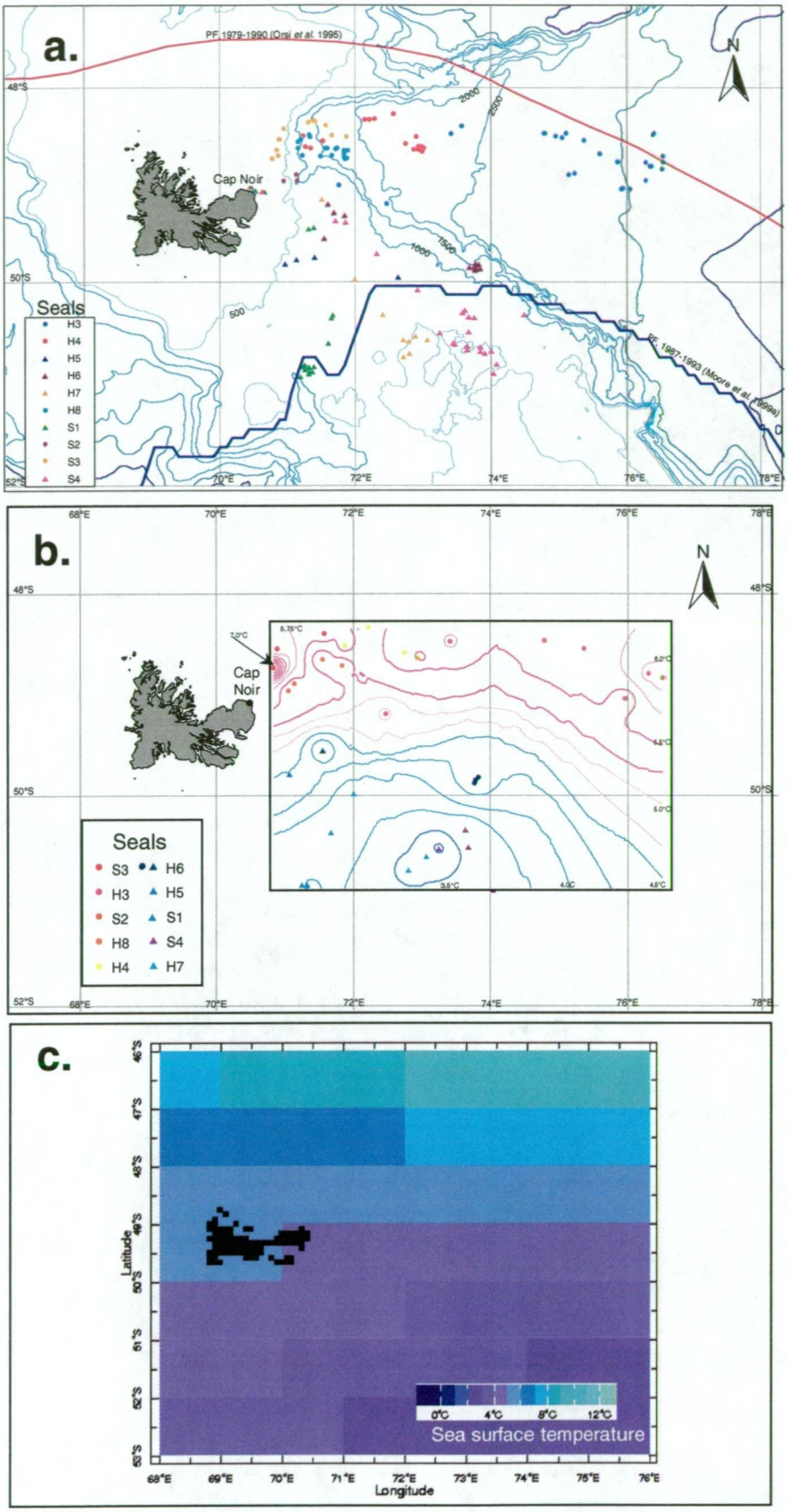


Figure 5.1 a. At-sea locations of 10 foraging fur seals in February 2000 from Cap Noir, Iles Kerguelen and local bathymetry (red and blue lines depict mean position of the Antarctic Polar Front-PF); *b.* MCSST contours (0.25°C) between nocturnal locations only (n=35) of the same 10 seals (circles denote foraging nights to the north and east, and triangles denote foraging nights to the south and southeast); *c.* weekly satellite SST in the Kerguelen region from 16-23 February 2000 measured by NOAA NCEP EMC CMB GLOBAL Reyn_SmithOlv1 weekly Sea Surface Temperature.

5.3.2 Physical/oceanographic parameters (ecoregions)

At the locations used by the seals, sea surface temperature ranged from 3.0-6.2°C, while chlorophyll-*a* concentration was generally high and relatively stable over the temporal and spatial scales used in this study (0.29-0.39 mg m^{-3}). MDS and cluster analysis (see Materials and methods) of the environmental variables at the three spatial scales were obtained with lowest stress levels for two environmental groupings (ecoregions) at the 1.0° spatial scale (Stress=0.028), although stress levels were low for all three spatial scales (stress<0.05, Fig. 5.2). Ecoregion 1 (warm and deep) was characterised by high mean MCSST (θ=5.4°C) and deep bathymetry (1872m; Table 5.2), whilst ecoregion 2 (cool and shallow) was characterised by cooler MCSST (θ=3.7°C) and shallower bathymetry (597m; Table 5.2). There was however, no variation in Chlorophyll-*a* concentration between the two regions, which is most likely related to the monthly averaging of patchily distributed Chlorophyll-*a* data.

Table 5.2: Physical parameters encountered by seals at nocturnal foraging sites.

	Chlorophyll-*a* (mg m^{-3})	Bathymetry (m)	MCSST 0.1° lat. (°C)	MCSST 0.5° lat. (°C)	MCSST 1.0° lat. (°C)
Ecoregion 1 (n=22)					
Mean	0.304±0.008	1872±192	5.38±0.15	5.44±0.14	5.60±0.19
Range	0.292-0.387	161-3129	3.75-6.150	4.28-7.35	4.27-7.35
Ecoregion 2 (n=13)					
Mean	0.297±0.005	597±26	3.61±0.12	3.71±0.10	3.89±0.17
Range	0.292-0.387	466-757	3.00-4.65	3.18-4.50	3.2-5.64

5.3.3 Diving activity within ecoregions

A total of 8386 dives were recorded for the 10 seals during the 35 nights at sea ($\overline{x}$=240±18 dives per night). The proportion of time spent diving by a seal on a particular night was highly variable (10-72%) as were mean dive depths (11.4-99.1 m). To test whether diving activity varied between ecoregions, the seven diving parameters (see Materials and methods) calculated for each seal on a nightly basis were included in a backwards-stepwise DFA at each spatial scale. Those diving parameters most influential in confirming the ecoregion groupings could then be identified. The assignment of foraging nights to the correct ecoregion group on the basis of the dive parameters was compared at the different spatial scales by Jackknife classification matrices (Table 5.3). The highest level of correct assignment to an ecoregion was achieved for two ecoregion groupings at the 0.5° spatial scale (Wilks' Lambda=0.382, Approx. $F_{2,32}$=21.796, P<0.0001), where 89% of nights were correctly reassigned to the original ecoregion group using two of the seven diving parameters: vertical depth (km hr^{-1}) and the proportion TSD at night (Table 5.3).

Higher cumulative vertical depths per hour were achieved in the warmer ecoregion 1 while spending proportionally less time diving during foraging nights than in the cooler ecoregion 2

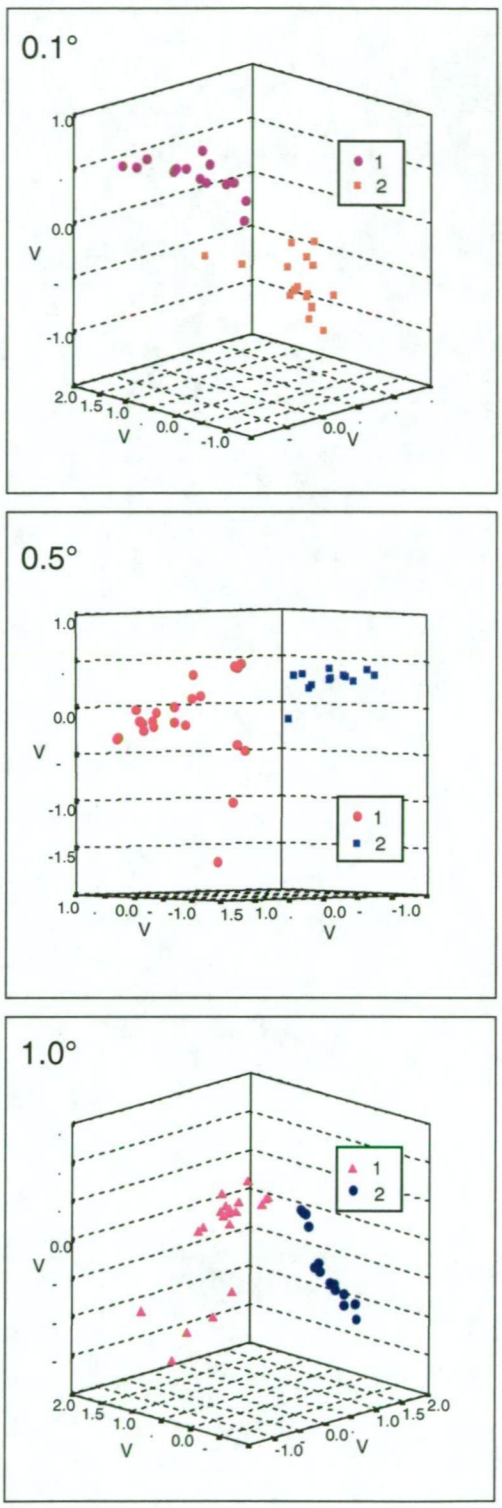


Figure 5.2 MDS plots at three spatial scales (0.1°, 0.5° and 1.0° latitude) indicating the relationship between environmental parameters (bathymetry, MCSST and chlorophyll-*a* concentration) during 35 foraging nights. Results for 2 cluster groups (ecoregions) are shown at each scale, while analyses were conducted for up to 6 ecoregions.

(Table 5.4). During nights spent in ecoregion 1 seals dived to greater mean depths, spent a lower proportion of time diving, had fewer dives per bout, and a lower proportion of overall dives in bouts than during nights spent in ecoregion 2 (Table 5.4). Those nights assigned to ecoregion 2 were characterised by more active diving behaviour. Dive frequency was considerably higher in ecoregion 2 with a further 4.2 min. per hour (7%) devoted to diving than in ecoregion 1.

Table 5.3: Discriminatory dive parameters of ecoregions identified by backwards DFA.

Spatial Scale	No. of ecoregion groups	Jackknife Classification assignment (%)	P	Discriminatory dive parameters
	2	74	0.001	2,7
	3	57	0.001	2,3
0.1°	4	57	<0.0001	2,3,7
	5	51	<0.0001	2,3,7
	6	49	<0.0001	2,3,7
	2	89**	<0.0001	4,7
	3	77	<0.0001	3,4,7
0.5°	4	57	<0.0001	3,4,7
	5	37	<0.0001	3,4,7
	6	49	<0.0001	3,4,7
	2	80	<0.0001	2,7
	3	77	<0.0001	2,3,7
1.0°	4	69	<0.0001	3,4,7
	5	54	<0.0001	3,4,7
	6	46	<0.0001	3,4,7

Dive parameter codes: 1- Dive freq.; 2- dive depth; 3- dive duration; 4- Vertical depth km hr^{-1}; 5-dives per bout; 6- Prop. dives in bouts and 7- Time spent diving ** best assignment to ecoregion

Table 5.4: Average measures of diving activity per night of seals foraging in the two ecoregions.

	Ecoregion 1 (warm & deep, n=22)		Ecoregion 2 (cool & shallow, n=13)	
Dive parameters	Mean	Range	Mean	Range
Dive frequency (hr^{-1})	22.3 ± 2.3	6.4-41.7	30.0 ± 2.6	13.5-42.5
Mean dive depth (m)	55.6 ± 4.8	11.4-99.1	34.5 ± 3.3	19.6-56.7
Mean dive duration (min)	1.4 ± 0.1	0.4-2.4	1.2 ± 0.1	0.7-1.8
Vertical depth (km hr^{-1})*	2.2 ± 0.2	0.4-3.3	2.0 ± 0.2	0.8-3.1
Dives per bout	8.8 ± 0.7	4.8-19.6	9.8 ± 0.6	6.4-14.6
Proportion dives in bouts	0.91 ± 0.03	0.45-1.0	0.95 ± 0.02	0.86-1.0
Proportion TSD*	0.47 ± 0.04	0.10-0.66	0.54 ± 0.03	0.34-0.72

* parameters identified by DFA, values ±SEM

5.3.4 TDR and MCSST comparisons

In order to examine the validity of using SST estimated by TDRs for temporal comparisons of nightly SST, log-transformed weekly MCSST measurements (SST_{Sat}) at the various foraging locations (0.1°x0.1°) were correlated with logged SST recorded by TDRs (SST_{TDR}; r_{35}=0.847, p<0.001). The relationship, which was not a 1:1 relationship, was also explained by the following regression equation: $SST_{TDR} = 0.594*SST_{Sat} + 0.588$ (r^2=0.718, $F_{1,33}$=87.414, P<0.001; Fig. 5.3). It appears that lower SST (<4.0°C) were slightly overestimated by TDRs, while readings >4°C were underestimated. The relationships between SST_{TDR} and SST_{Sat}

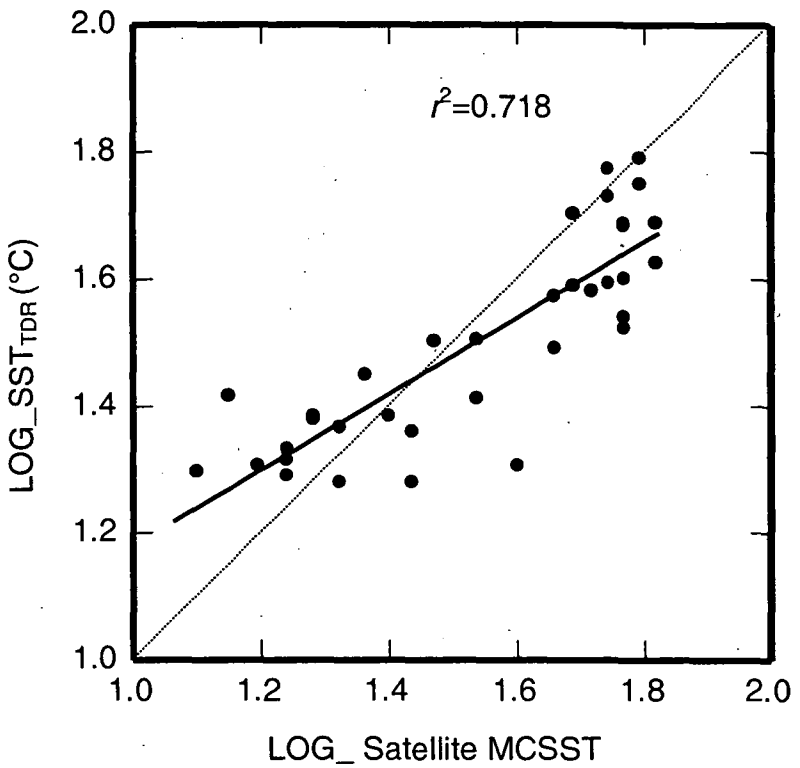


Figure 5.3 The relationship between SST recorded by satellite (0.1x0.1° latitude) and time-depth recorders on Antarctic fur seals at 35 nocturnal foraging locations.

at the other spatial scales (0.5° and 1.0°), while also significant, were more variable (r^2=0.612 and 0.476 respectively).

5.3.5 Temporal variation in MCSST during a foraging trip

Sea surface temperatures for all nights during the 10 seal' foraging trips (n=75 recorded by TDR) were extracted in order to compare SST during sequential nights within a foraging trip as well as over the entire foraging trip (Fig. 5.4), as this information was not available from satellite location data. Two seals foraging in ecoregion 1 (H3 and H4) spent the majority of their time in regions of warm SST (θ>~5°C) although H3 did visit an area of cooler SST on day 10 of the foraging trip (Fig. 5.4).

The other seals foraging in ecoregion 1 (H6, H8, S2 and S3), while having shorter foraging trips, spent much of their time in waters of comparably high SST (θ=4.5-5.0°C). Those seals assigned to the cooler, ecoregion 2 spent the majority of their foraging time in areas where SSTs were comparable over the duration of the foraging trip (θ=3.5-4.0°C). Any increases in SST occurred during either the first or last nights of the foraging trip, probably in close proximity to the colony. H6 was the only seal to record foraging nights in both ecoregions (Fig. 5.4) with the first night of the trip occurring in ecoregion 2 while the other three nights were assigned by DFA to ecoregion 1. This seal spent only 50% of the time at night diving while in Ecoregion 1 compared with 65±0.02% in ecoregion 2. Vertical depth per hour of night attained by H6 also differed considerably between ecoregions at 1.9 and 3.2 km hr^{-1} respectively. As SST encountered by H6 were similar between ecoregions it appears that bathymetry and diving behaviour of the seal in the two areas accounted for the assignment to both ecoregions. Thus it would appear that the diving activity of a particular individual may change in response to changing environmental conditions even within a foraging trip.

There appears to be a positive relationship between mean nightly SST_{TDR} per foraging trip and trip duration for those seals which spent all of their time foraging in ecoregion 1 (Fig. 5.5), however overall the relationship was not statistically significant ($F_{1,8}$=0.002, r^2=0.00, P=0.964).

5.3.6 Temperature profiles

The mean temperature-depth profiles of seals from the two regions were also compared using temperature values recorded by the TDR (Fig. 5.6). Temperatures recorded in the upper 100 m were more variable for seals foraging in the warmer ecoregion 1, where deeper dives constituted a large proportion of diving activity (Fig. 5.6). Although dives of up to 180 m depth were recorded, the number of dives deeper than 100 m constituted only 2.8±1.4% and 1.3±0.8% of dives in ecoregions 1 and 2 respectively. Below this depth, temperatures dropped more swiftly indicating a change in thermal structure of the water. The temperature profile of seals from

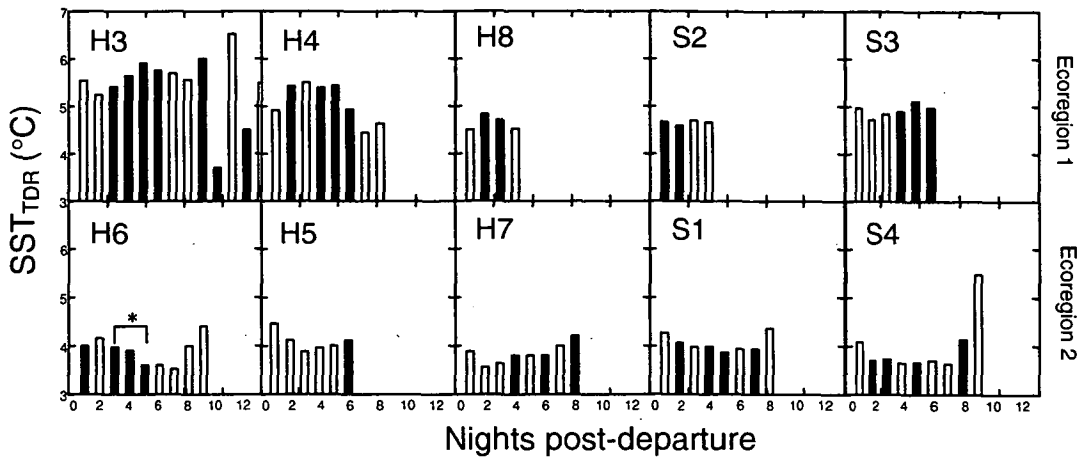


Figure 5.4 Nightly SST_{TDR} throughout the foraging trip by ecoregion. (Black bars represent nights during which at-sea locations were recorded): * denotes foraging nights assigned to ecoregion 1 by DFA (H6 included in ecoregion 1).

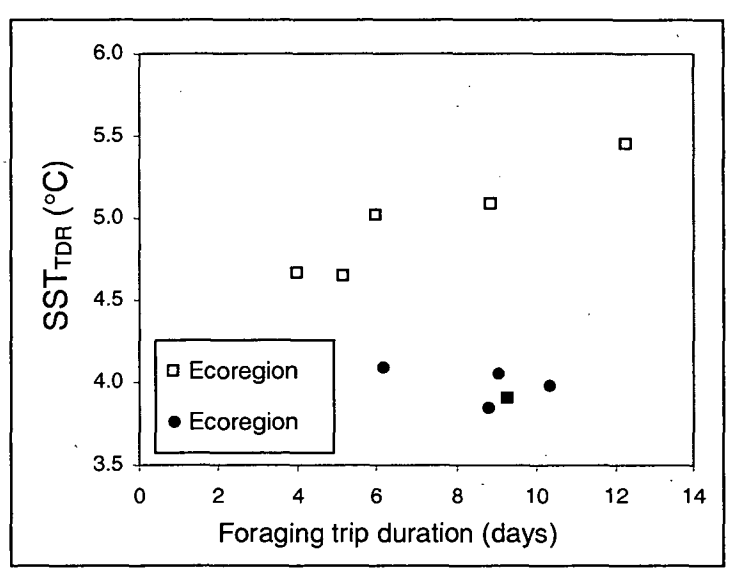


Figure 5.5 The relationship between trip duration and mean nightly SST as measured by TDR during the foraging trip. The filled black square denotes H6, the seal whose diving activity spanned both ecoregions.

ecoregion 2 was more consistent at shallow depth (3.7-4.0°C), with a change in temperature apparent at a similar depth of approximately 100 m (Fig. 5.6).

5.3.7 Foraging efficiency and pup provisioning

Energy transfer to the pup could be compared between females utilising the different ecoregions only on a per foraging trip basis. Absolute and daily mass gained by the pup (PMG) during the attendance period following the maternal foraging trip, were related to various foraging parameters. Maximum distance travelled from the colony ($F1,_7$=43.26, r^2=0.841, P <0.01) and the proportional mass gain of pups ($F_{1,7}$= 71.498, r^2=0.898, P <0.01) were both significantly, positively related to foraging trip duration. Proportional mass gain represents the percentage of the pup's arrival mass gained during the mother's shore attendance.

Mean depth during a foraging trip was negatively related to absolute pup mass gain (Fig. 5.7*a*, $F_{1,7}$=25.74, r^2=0.756; P <0.01) and the duration of the foraging trip (Fig. 5.7*b*, $F_{1,7}$=11.29, r^2=0.563; P <0.05). Once the duration of the foraging cycle (FT & SB) was taken into account, the relationship between daily PMG per foraging cycle and mean depth remained significant ($F_{1,7}$=10.329, r^2=0.538, P <0.05).

Both absolute PMG (2.42±0.35kg) and the daily PMG per foraging cycle (231±19g d^{-1}) were similar for seals foraging in both the warm and deep ecoregion 1, and cool and shallow ecoregion 2, ($t_{7,[0.05]}$= -0.766, P=0.441 and $t_{7,[0.05]}$= -1.211, P=0.262, respectively). PMG however, tended to be less variable for seals whose mothers foraged in ecoregion 2 to the south-east (Fig 5.7*c*). Thus, the foraging efficiency of mothers feeding in the two ecoregions was similar, despite differences in environmental parameters and diving activity recorded.

Daily PMG was unrelated to average nightly bathymetry (r_9=0.185, P=0.635), while the relationship between PMG, mean depth and MCSST is more clearly illustrated in 3-dimensions (Fig. 5.7*d*). Interestingly, the rate of daily PMG per foraging cycle and MCSST (0.5° latitude) had an almost significant, negative correlation (r_9=-0.642, Bonferroni correction P= 0.062). However, when this relationship was tested using mean nightly SST_{TDR} per foraging trip, the correlation was less compelling (r_9=-0.313, P=0.412).

5.4 Discussion

This study examined the relationships between physical and oceanographic parameters on a fine scale (0.1°-1.0° latitude) in regions used by Antarctic fur seals, and their diving behaviour whilst foraging. Differences in habitat characterised by hydrography and bottom topography were strongly associated with differences in the nocturnal diving activity of seals at the 0.5° latitude scale, and in the provisioning of pups. The links between environmental conditions in the short-

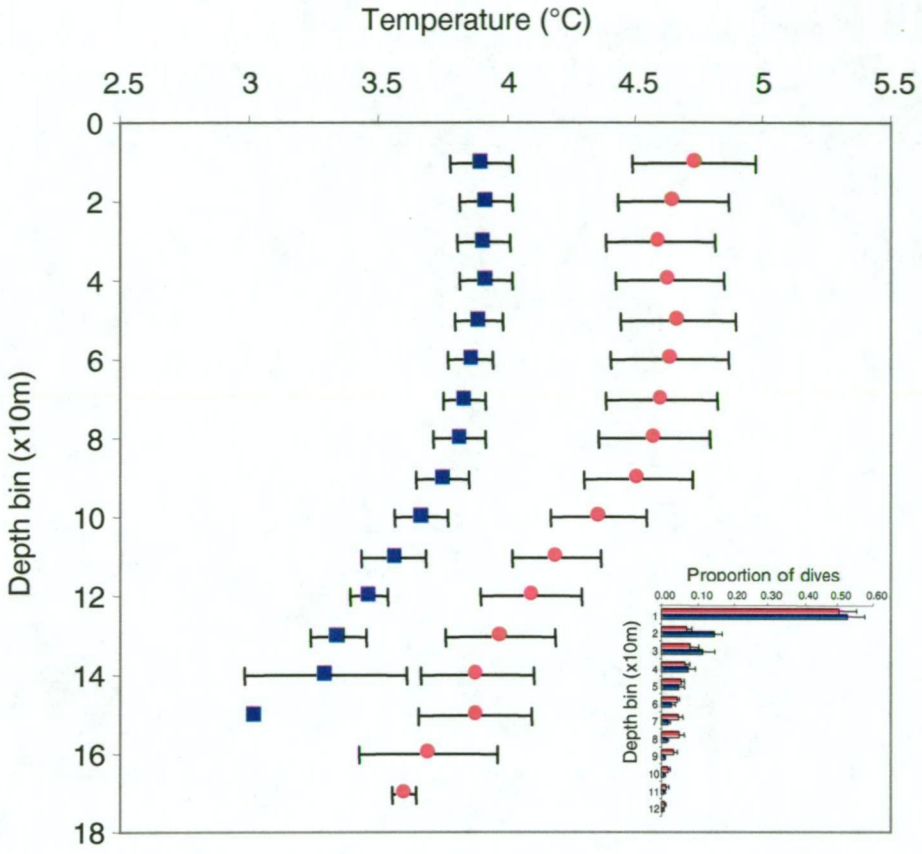


Figure 5.6 Mean temperature-depth profiles during nightly dives by Antarctic fur seals in ecoregion 1 (red circles) and ecoregion 2 (blue squares). Inset diagram depicts the proportion of dives assigned to 10m depth bins per ecoregion.

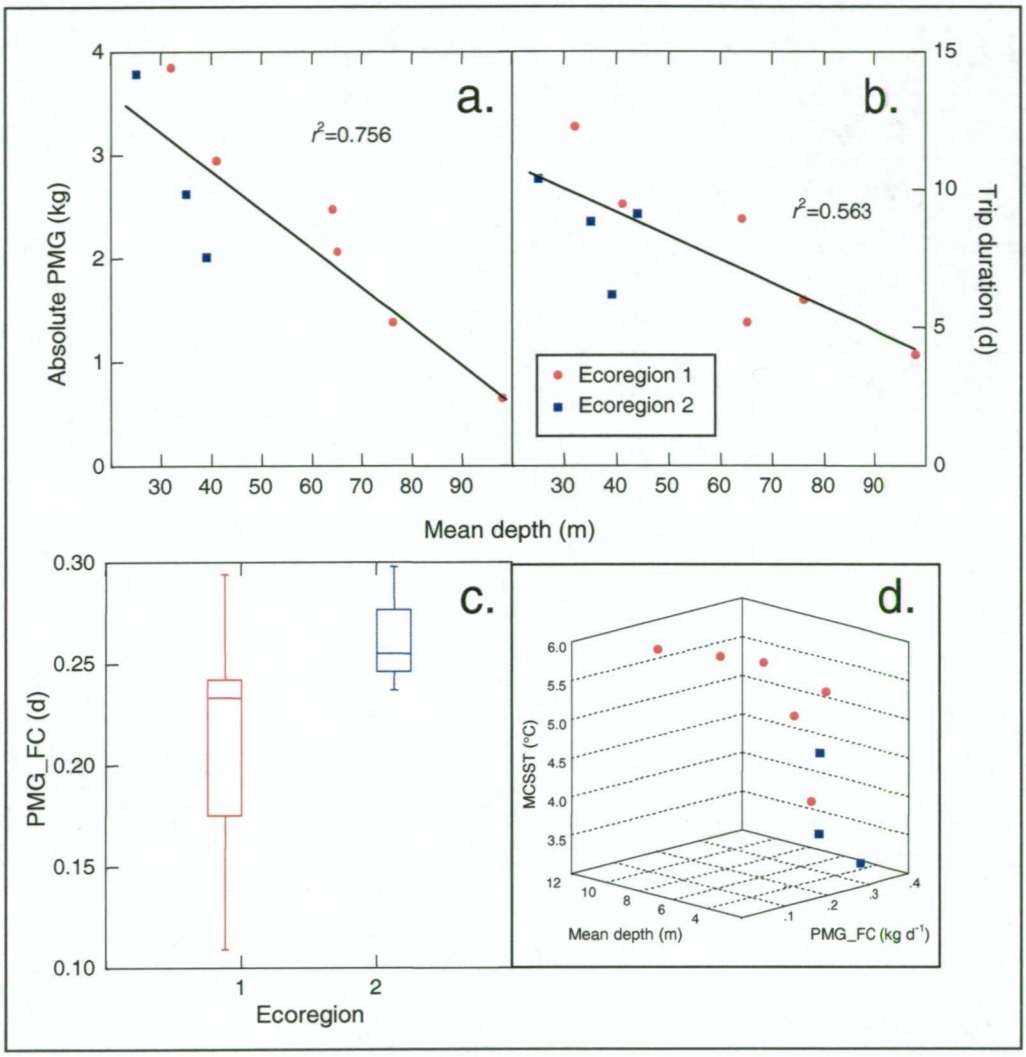


Figure 5.7 (a-d) The relationship between mean depth during a foraging trip and (*a*) absolute pup mass gain and (*b*) trip duration; (c*)* mean differences in daily mass gain (PMG) throughout the foraging cycle (FC) with mothers foraging in ecoregion 1 (red) and 2 (blue); and (*d)* 3-dimensional relationship between mean depth, SST and daily mass gain of the pup (kg d^{-1}).

term, the foraging behaviour of seals in waters of the dynamic and variable Polar Frontal Zone and the subsequent consequences for their pups in terms of energy delivery are discussed.

5.4.1 Environmental variation and habitat utilisation

The at-sea distribution of female Antarctic fur seals in February 2000 could be divided into those foraging to the north-east and east of the colony and those which headed in a south-easterly direction (Bonadonna *et al.* 2000 & 2001). Seals foraged over oceanic and shelf break waters but spent little time diving over the continental shelf (<500m), in accordance with conspecifics studied at Îles Kerguelen in 1998 (Guinet *et al.* 2001), at South Georgia (Boyd *et al.* 1998; McCafferty *et al.* 1998; McCafferty *et al.* 1999); Macquarie Island (Robinson 2002) and at the Antarctic Peninsula (Goebel *et al.* 2000). In 2000 (this study) the bottom topography of the two ecoregions used by seals varied considerably. The Kerguelen Plateau extends from the archipelago in a south-easterly direction for several hundred nautical miles. Hence, nights of seal foraging activity in ecoregion 2, south-east of Cap Noir, are associated with cool SST (3.7°C) over the continental shelf edge of the Plateau (~600m). This region, is also regularly used by female Antarctic fur seals breeding at Heard Island (Green 1997; Simon Goldsworthy, Personal Communication). The temperatures in this area were consistent with the surface expression of waters of the Polar Front (see Koudil *et al.* 2000), although in the Kerguelen region, subsurface and surface expressions of the PF are regularly separated by up to 8° of latitude (Sparrow and Heywood 1996). Generally, the range of SST above the PF between September and February are in the vicinity of 1.6-2.5 to 4.8-5.2°C (Belkin and Gordon 1996). Foraging activity occurring in ecoregion 1, however, tended to be associated with deeper (1870 m) and warmer (5.4°C) pelagic waters on average. Thus the static variable, bathymetry, and SST on a weekly temporal scale at all three spatial scales, accounted for the differences in the ecoregions encountered by seals. In February 2000, we were unable to detect any differences in surface chlorphyll-a concentration and likely phytoplankton abundance. There are several factors, which may have resulted in this finding. Firstly, due to consistent cloud cover in these latitudes, data were averaged monthly over a region of 81km^2. Thus the resolution of the data was probably insufficient to detect finer scale variability in phytoplankton abundance. However it is also likely that marine productivity was generally high across the study area in February 2000. Blain *et al.* (2001) have shown that iron input from the plateau, and a favourable light-mixing regime in summer induce high chlorophyll plumes downstream of the Kerguelen Plateau (Fig. 5.8).

5.4.2 Diving activity in relation to spatial scale

The most compelling finding of the study was the strong relationship between nightly diving activity and the presence of seals in the two different ecoregions. The reliability of the relationship was strongest at the 0.5° latitude scale for MCSST, although it was also relatively

strong for two ecoregions at the 0.1° and 1.0° scales. The differences observed in the foraging behaviour of seals in the two ecoregions suggest that prey distribution and perhaps composition of these waters also differed, consequently influencing the diving activity of the seals. Foraging to north-east and east of the archipelago, in waters that were consistently warmer than the second ecoregion, comprised dives to greater average depths, deeper vertical depths per hour, for shorter time periods. Dives in ecoregion 2, to the south-east, were shallower, yet occupied a greater proportion of the night in terms of time spent diving.

The temperature profiles of seals foraging over oceanic waters to the north-east, however, appear to represent waters of the PFZ (see Field *et al.* 2001). Warm sea surface temperatures (4.5-5.0°C) remained relatively stable to approximately 100m, descending to less than 4°C by 150m depth. The relative homogeneity of temperatures in the upper water column may be indicative of some mixing of water masses. The mixed layer depth (MLD) ranges from 50-200m within the vicinity of the islands, depending upon the season (Bucciarelli *et al.* 2001). To the south of Kerguelen (50°40'S, 68°25'E), Park *et al.* (1998) have recorded an average mixed layer depth (MLD) of only 60m in January, by averaging monthly values from May 1991 to December 1994. MLD is defined as the depth at which a density difference of 0.02 (σ_θ) occurs between surface waters and waters at depth (Park *et al.* 1998). This depth generally decreases in a pole-ward direction (Park *et al.* 1998; Koudil *et al.* 2000). Thus, the deeper foraging dives made by seals to the north-east may reflect the MLD in that region, with seals further south in the cooler ecoregion encountering a shallower MLD. Biological productivity is known to be greatest within the mixed layer (Mann and Lazier 1991 in McCafferty *et al.* 1999) and it has been suggested that prey may be predictably concentrated below the surface mixed layer (SML) at the thermocline (Charrassin and Bost 2001), or at discontinuities between water masses (Boyd and Arnbom 1991). Additionally, significant changes in phytoplankton growth and abundance a few 10's of kms in the north-south direction within the PFZ are known to occur (Abbott *et al.* 2000), perhaps further affecting prey species composition and distribution. One species known to minimise time within the surface mixed layer are king penguins breeding at the Crozet Archipelago, which prefer to dive in and below the depth of the thermocline (Charrassin and Bost 2001). King penguins, similar to Antarctic fur seals, feed primarily on myctophid fish (Cherel *et al.* 1996), however their diving is generally restricted to daylight hours, occurring rarely at night (Bost *et al.* 2002). Consequently they must attain greater mean depths (~200 m) when foraging than fur seals (Charrassin and Bost 2001).

5.4.3 Temporal variability in MCSST

Sea surface temperature measurements recorded by TDR correlated reasonably well with satellite measurements over similar a weekly time scale. Boyd (2001) studying Antarctic fur seals and oceanographic features at South Georgia were unable to find a relationship between

satellite SST measures and TDR SST values at any spatial scale which they attributed to cloud cover and the use of surface reflectance by satellites, as opposed to temperature measured over the first 5 m of the water column with TDRs. Our study, at Îles Kerguelen, shows that temperatures recorded by fur seals at sea in this region of the Southern Ocean, are indicative of satellite estimates of SST, .

After an initial decrease in SST on departing the colony, nightly SST measured by TDR tended to remain relatively stable within an ecoregion. Of the ten individuals studied in February 2000, only one seal appeared to switch between ecoregions during the same foraging trip. Even seals conducting long, looping and possibly exploratory foraging trips (Bonadonna *et al.* 2000) remained in the one ecoregion for the majority of the trip. McCafferty *et al.* (1999) studying temporal variability in SST during the foraging trip of Antarctic fur seals at South Georgia, showed that SST and percentage time spent diving both varied in response to female identity and stage of the foraging trip, depending upon the months and years tested. At South Georgia seals may travel up to 350km to reach warmer waters of the PF to the north-west of the island (1998), whereas at Kerguelen the waters of the PF are generally more accessible to seals and perhaps more homogenous to the north or south of the PF.

5.4.4 Implications for prey availability and foraging success

The main prey of Antarctic fur seals in the Kerguelen region, mesopelagic myctophid fish (Cherel *et al.* 1997; Chapter 4), are highly abundant in the PFZ (Duhamel *et al.* 2000) and concentrated at the PF (Sabourenkov 1991), which reaches its northernmost position at 46-47°S near Îles Kerguelen (Belkin and Gordon 1996). The nocturnal diving behaviour of the seals (Chapter 2), reflects the diel migration of myctophids (Duhamel *et al.* 2000) and that of their zooplankton prey. Thus, differences in prey species consumed by seals foraging at different depths within the two ecoregions may be expected. The higher incidence of dives in bouts (95%) suggests that the cooler waters of ecoregion 2 may also have been more productive in terms of prey availability. Foraging seals must locate their migratory prey in three-dimensions and little is currently understood about the behaviour of myctophid schools on a fine scale. However, it appears that the behaviour and distribution of prey are sufficiently influenced by differences in bottom topography, associated SST and perhaps levels of upwelling in the two ecoregions to affect the diving behaviour of seals.

A high degree of uniformity in population diet samples collected in February 2000 was evident, with myctophids accounting for around 95% by number of all fish and cephalopod prey (Chapter 4). To assess individual dietary preferences, the fatty acid composition of milk samples (Chapter 4) available for six of the fur seals in the present study, were compared between ecoregions (Fig. 5.9). Although only limited sample sizes were available, there was little

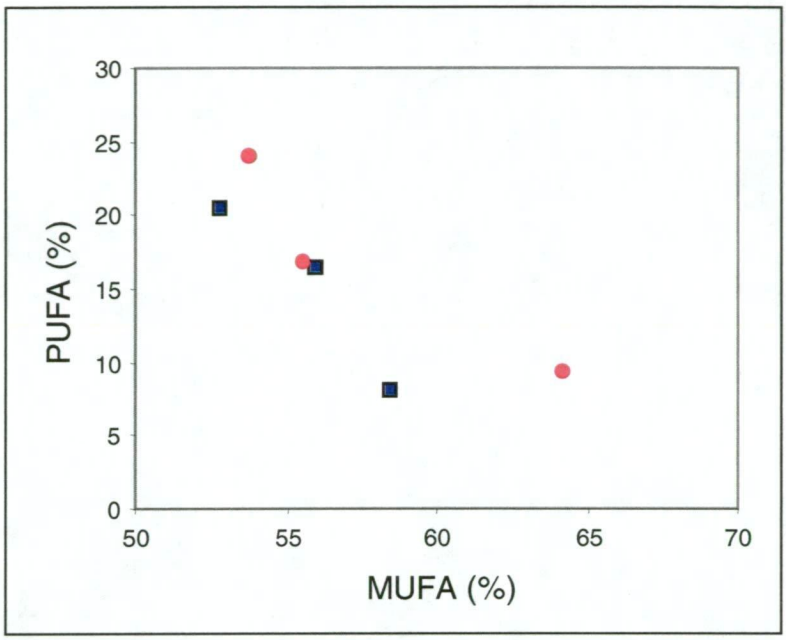


Figure 5.9 The relationship between mono- and polyunsaturated fatty acids levels in female Antarctic fur seals foraging in ecoregion 1 (red circles) and ecoregion 2 (blue squares).

difference in fatty acid composition between ecoregions. High monounsaturated levels (MUFAs), indicative of myctophids (Saito and Murata 1998; Chapter 4), were common (53-64%). While these results are inconclusive, the variation in FA composition recorded within and between ecoregions implies that dietary preferences probably occur at the level of the individual rather than purely in response to changing topography and hydrographic features typical of the two ecoregions. Evidence of the relationship between fine scale prey availability and selectivity and hydrographic features have, however, been identified for some seabirds. Nel *et al.* (2001) have recently shown that grey-headed albatross use warm and cold eddies associated with the PF at Marion Island and have linked specific prey items, such as predatory fish and squid (*Martialia hyadesi*), to the occurrence of these hydrographic features.

The foraging behaviour adopted by seals heading south to the region of the PF seems most costly in terms of foraging effort. Seals in this group travelled, on average slightly further (245 *cf.* 219 km) from the colony and spent more of their time at sea diving. Yet these seals managed to provision their pups at similar rates to seals foraging in ecoregion 1 in PFZ waters. It is possible that increased prey availability is associated with a shallower MLD to the south-east of Kerguelen and that reduced rates of intra-specific competition are positive trade-off associated with this strategy of foraging, as the colony-preferred direction over three years (1998-2000) was to the north-east of Cap Noir (Bonadonna *et al.* 2000 and 2001). It is equally possible that seals foraging more deeply in PFZ waters (ecoregion 1) encountered prey species less frequently but that those prey were perhaps of higher calorific value (Chapter 4). That female seals exhibited similar rates of foraging efficiency regardless of the at-sea conditions encountered, and associated changes in diving behaviour, further confirms the flexibility in foraging strategies previously identified for this species (Chapter 2; Bonadonna *et al.* 2000). This study addressed the linkages between environmental conditions, diving behaviour and pup provisioning on a nightly and single foraging trip scale, and the costs and benefits associated with the use of either foraging behaviour may be cumulative, accruing over the duration of many sequential foraging trips. However, under the variable conditions encountered in February 2000 at Îles Kerguelen, at least in the short-term, it appears that seals were capable of adjusting their-at sea behaviour to effectively account for this variability and effectively provision their pups.

5.4.5 Conclusions

Fine scale variations in the physical marine environment, particularly in sea surface temperature and bathymetry, will affect the foraging behaviour of Antarctic fur seals on a nightly basis, with seals in one region exhibiting higher rates of diving effort, spending more of their time diving to shallower depths in a region typified by cool SST and shallow bathymetry than seals in warmer and deeper waters. However, in what appeared to be a year of relatively high marine productivity at Îles Kerguelen, seals were able to deliver similar quantities of milk to their pups despite the discrepancies in diving activity and trip duration between the two groups.

5.5 SUMMARY

- the diving activity and foraging distribution of 10 female Antarctic fur seals in February 2000 were examined with respect to SST, chlorophyll distribution and bathymetry
- nightly foraging activity of five seals occurred in oceanic waters (1870 m) with relatively warm SST of 5.4°C to the north and east of the colony, whilst four of the remaining seals travelled to the south-east to waters typical of the surface expression of the Polar Front (3.7°C) located over the continental shelf break (597 m). One seal foraged in both regions during the course of a single foraging trip
- the diving behaviour of seals clearly differed between regions, with diving activity within the warmer ecoregion 1 being characterised by deep dives (55.5m), a relatively low proportion of time spent diving and high hourly vertical depths
- conversely, diving behaviour within the cooler ecoregion 2 was, on average, to shallower depths (34.5m), while proportionately more of the time was spent diving (54% cf. 47%)
- despite differences in environmental conditions encountered during foraging trips and consequent changes in diving activity, the foraging efficiency of mothers, in terms of daily pup mass gain per foraging cycle, was similar in both ecoregions

Chapter 6

Environmental determinants of maternal energy acquisition and allocation

6.1 Introduction

Lactation is commonly viewed as one of the more energetically expensive phases of a female mammal's life (Oftedal 1984) relative to maintenance costs, through the provisioning of milk to ensure offspring growth (Lee *et al.* 1991). Lactating northern fur seals (*Callorhinus ursinus*), for example, consume 1.6 times more prey than non-lactating individuals during this period (Perez and Mooney 1986). While suckling, a mother makes many decisions concerning the allocation of time for foraging to meet her own energetic requirements, and for nursing young. Such choices may vary in relation to food availability, maternal age and experience and age of offspring. For a given species, and different populations within the same species, where the availability of food is highly variable in space and time, these decisions may be crucial, affecting current and possibly future reproductive success, and in extreme instances even maternal survival (Trites 1991; Lunn *at al.* 1993). Consequently, individual mothers may have flexible provisioning and weaning strategies in response to local environmental conditions (Lee *et al.* 1991).

In the pinniped family, the distribution of which extends from polar regions, including the most southerly breeding mammal group in the Antarctic (Testa and Scotton 1999), to species inhabiting equatorial regions (Trillmich 1986a; Trillmich 1986b; Trillmich 1987), has evolved two distinct life histories, enabling them to effectively resolve the spatial separation between breeding sites and feeding areas. Phocids, known as capital breeders (Stearns 1992; Boyd 2000), accumulate large adipose stores prior to breeding, which they then convert to lipid-rich milk during a short lactation period (4-70 days), suckling their pup continuously on land or ice from birth to weaning without foraging (Bonner 1984; Bowen *et al.* 1985; Kovacs and Lavigne 1986). Their generally large body size (e.g. up to 800kg; McCann *et al.* 1989) coupled with vast distance between breeding and foraging sites (e.g. 3100km for southern elephant seals, Jonker and Bester 1994), means that the physiological demands of lactation and the consequences of variability in prey resources are temporally and spatially separated (Bonner 1984). Conversely, otariids (fur seals and sea lions), which are considerably smaller (from 25kg), combine foraging activity with the raising of their single offspring by interspersing periods of foraging at sea with periods ashore (termed income breeders, Stearns 1992). Consequently they may be less well buffered against environmental variability than capital breeders (Boyd 2000). In sub-polar regions were resource availability is seasonal, but predictable and abundant, the lactation period of otariids is short at four months (e.g. Antarctic and northern fur seals), whereas in equatorially breeding Galapagos fur seals (*Arctocephalus galapagoensis*) lactation may extend to three years because food is less abundant and more unpredictable (Trillmich 1986a; Trillmich and Dellinger 1991; see Gentry and Kooyman 1986). Otariids can be considered central place foragers (Orians and

Pearson 1979), as mothers must return regularly to breeding sites in order to feed their young. As such, the maximum foraging range attainable during feeding trips and the maximum time allocated to foraging are constrained by the physiological demands of the pup. Mothers should optimise the time allocated to various activities in order to maximise the rate of food delivery to young under all conditions (Houston *et al.* 1996 in Boyd 1999). However, in years where environmental perturbations affect prey availability and the ability of otariid mothers to locate prey during lactation, catastrophic repercussions for breeding success can occur, with up to nearly 100% pup mortality (Croxall *et al.* 1988; Trillmich and Dellinger 1991; Boyd *et al.* 1995).

The Antarctic fur seal is a tractable model for examining the relationship between environmentally induced fluctuations in prey availability, foraging behaviour and subsequent breeding success. It has a circumpolar breeding distribution, which includes the majority of sub-Antarctic islands, spanning the Southern Ocean from Marion Island (46°54'S, 37°45'E) to the Antarctic Peninsula (62°29'S, 60°47'W). Across this distribution, hydrographic features, climatic conditions and prey species composition vary considerably (Tynan 1998; Moore *et al.* 1999a; Abbott *et al.* 2001; Hunt *et al.* 2001). Variability in the marine environment during the brief lactation period may rapidly be translated to longer search times and reduced provisioning and growth rates for young, as has been observed at South Georgia (Lunn and Boyd 1993a; Lunn *et al.* 1993; Boyd *et al.* 1994).

In the southern Indian Ocean, Antarctic fur seals feed primarily on the Myctophid family of nocturnally surface migrating mesopelagic fish, which are rich in energy and highly abundant in the Antarctic Polar Frontal Zone (Cherel *et al.* 1997; Klages and Bester 1998; Duhamel *et al.* 2000; Bost *et al.* 2002; Chapter 4). Movements of the Antarctic Polar Front by 1-2° north or south occur inter-annually in this sector of the Southern Ocean (Moore *et al.* 1999a), potentially affecting both the abundance and species composition of prey available within the foraging range of Antarctic fur seals. One of the main objectives of a three-year multidisciplinary study examining the myctophid predator-prey ecosystem at Îles Kerguelen, was to determine whether the foraging behaviour and consequent energy acquisition of female Antarctic fur seals was responsive to changes in environmental conditions and subsequent marine productivity. If such changes were evident, were increased costs of foraging translated directly to the pup in terms of reduced provisioning rates, or were females able to compensate by increasing the quality and/or quantity of resources per suckling event (see Trillmich and Lechner 1986; Hofer and East 1993)? The allocation of resources to the pup may also vary in relation to sex has been observed in this species on Heard Island, where male pups grew faster than females (Goldsworthy 1995). Parental

investment theory in sexually dimorphic species predicts that a parent should invest greater resources in offspring of the sex that is made fitter by receiving greater than average investment (Maynard-Smith 1980), which in polygynous mating systems, is usually the male. Therefore, we also investigated the inter-annual variability in the transfer of energy to the pup at Îles Kerguelen in relation to possible sex-based differences.

The at-sea distribution and foraging effort of lactating seals was studied over austral summers between 1998 and 2000 by the concurrent use of satellite transmitters and time-depth recorders. Inter-annual variability in these parameters were related to changes in oceanography, prey availability and the dietary preferences of seals. Provisioning rates, indicies of foraging efficiency and subsequent growth rates of pups were also compared between years and examined in relation to maternal and environmental parameters (chlorophyll-a concentration, sea surface temperature and bathymetry).

6.2 Materials and methods

6.2.1 Study site

The study was conducted at Cap Noir (49°07'S, 70°45'E) on the Courbet Peninsula, Kerguelen Archipelago. These islands are located near the Antarctic Polar Front (PF) and support an increasing population of Antarctic fur seals. At Îles Nuageuses to the northwest of the archipelago an increase of 17% per annum from the 1960s to the 1980s has led to the present estimate of over 10 000 seals (Jouventin and Stonehouse 1985; Guinet *et al.* 1996). At Cap Noir seals were first recorded breeding in 1984 (Bester and Roux 1986) after their virtual extinction in the 19th Century (Budd and Downes 1969). Pup counts conducted at Cap Noir in late January 1999 and 2000 produced estimates of pup production ranging between 750 and 800 individuals per year (Chapter 1).

The foraging behaviour of lactating adult female fur seals and the allocation of resources to the pup (body condition, growth and daily mass gain), were studied during the 1998 (4 Feb. 1998 – 13 Mar. 1998), 1999 (21 Nov. 1998- 5 Mar. 1999) and 2000 (11 Dec. 1999 – 15 Mar. 2000) austral breeding seasons. For comparative purposes we have generally limited data to the same period each year (February and March).

6.2.2 Environmental data

Bathymetric data at the foraging locations of seals (see below) were extracted from the ETOPO5 database (5' x 5' resolution). Weekly MCSST (°C) and monthly Chlorophyll-a concentration (mg m^{-3}) data were obtained from the PODAAC (Physical Oceanography Distributed Active Archive Center) by ftp on *ftp://podaac.jpl.nasa.gov/pub/sea_surface_temperature/avhrr/mcsst/* and SeaWIFS respectively, for an area within a 750km radius of

the colony at Cap Noir (see chapter 5 Materials and methods). This area was selected as it encompassed the maximum foraging range used by any seal during the study. Monthly Sea Surface Temperature Anomaly data (SSTA) was estimated from blended ship, buoy and bias-corrected satellite data (Reynolds and Smith 1994) from 1991 to 2002, extracted from the National Centres for Environmental Prediction (NCEP) Reynolds analyses at NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv1/.monthly/.ssta/. Data are produced weekly on a one-degree grid and were obtained for a region bounded by 46.5°S 69.5°E and 52.5°S 75.5°E, which encompassed the foraging zones of the seals.

6.2.3 Maternal energy acquisition

Several parameters, which function as proxies for rates of maternal energy acquisition, were measured in each of the three years. These include: maternal attendance behaviour, the at-sea distribution and diving activity of female seals, dietary preferences, indices of prey availability and body condition of female seals.

6.2.3.1 Attendance patterns

VHF transmitters (150-151 MHz, 1s transmission rate) were attached to 20 females in each year in order to monitor the attendance behaviour of a group of seals that were independent of all other experimental procedures. Female seals were monitored from 7 February to mid-March, 1998, and from late December until March in 1999 and 2000. Only data post 19 January were included in inter-annual comparisons. A DCCII radio receiver (ATS, Minnesota, USA), powered by a 12V battery, and an antenna located within the colony scanned all frequencies for 30s every 10 min. recording the presence/absence of seals within the colony. Females were captured with a hoop net, measured in a straight line from nose to tail to the nearest centimeter, weighed to the nearest 0.2 kg with 50x0.2 kg capacity scale (Salter Industrial Measurements Ltd) and then placed on a restraint board. Either back-mounted transmitters (50x30x15 mm, 25 g, Sirtrack Pty Ltd, NZ) were attached to the fur on the seal's rump with a quick-setting two-part epoxy glue (AW 2101, Ciba Specialty Chemicals), or flipper tag VHF transmitters (Sirtrack Pty Ltd, NZ) mounted on Dalton Roto tags (35x25x15 mm, 26.3 g , Woolgoolga, NSW, Australia) were deployed in the trailing edge of seals' fore-flippers (Sirtrack, NZ). Data were downloaded onto a laptop computer every five days. At the end of each field season data for each individual were combined and shore bout (SB) and foraging trip durations (FTD) were calculated by manually screening the data for the seals' arrival and departure times. Attendance behaviour did not vary between deployment methods in 1998, and as such all data have been pooled. Any mothers whose pups died (n=3), who lost the transmitter during the study period (n=1), or whose transmitter malfunctioned (n=1), were excluded from analyses, thus yielding 20, 19 and 16 mother-pup pairs in 1998, 1999 and 2000 respectively.

6.2.3.2 At-sea distribution & foraging activity

In 1998, platform terminal transmitters (ST-10 PTT, Telonics Pty Ltd, Arizona, USA packaged by Sirtrack, NZ) linked to the ARGOS satellite system were mounted with a Mk 5 time-depth recorder (TDR, Wildlife Computers, Washington, USA). In 1999 and 2000 the package consisted of a Mk7 TDR (Wildlife Computers, Washington, USA) mounted on the PTT (110x42x25 mm, 150g). Packages were deployed on 12 females in 1998, 11 females in 1999 and 12 females in 2000. All packages were shaped to reduce drag (Figure 6.1) and were attached by plastic cables ties to a nylon-webbing strap, which was attached dorsally to the seal on the midline between the scapulae with two-part araldite (AW 2101, Ciba Specialty Chemicals, Switzerland). Animals were marked with individual numbers on the rump with peroxide hair-dye (Bristol Myers-Squibb, Rydalmere, Australia) before being released with their pup. The colony was checked at least twice daily for the return of marked females.

The TDRs were programmed to record depth (±1 m) every 5 s throughout the course of a single foraging trip. Temperature (±0.1°C) was also recorded every 5 s for all seals equipped with Mk7 TDRs in 1999 and 2000. In 1998, where the memory of three Mk5 TDRs (n=6 of 11 deployments) was insufficient for the long duration of trips, temperature was sampled each 5 s (n=2), 30 s (n=3), 60 s (n=5) or 300 s (n=1). Mean nightly SST were calculated from temperature records as described in Chapter 5. Dive data were extracted from the TDRs, corrected for surface drift and analysed as described in Chapter 2. The spatial distribution of diving activity was calculated each year using custom-made software (Laurent Dubroca, CEBC-CNRS), which attributed time spent diving as recorded by an individual's TDR to a particular foraging location as indicated by the PTT derived locations. Only ARGOS locations of accuracy class 0-3 were used in analyses (see Bonadonna *et al.* 2000). The amount of time spent diving in each 0.1°x0.1° (11.1 km latitude x7.3 km longitude) grid area encompassing the foraging zones of seals, was calculated and mapped using ArcView GIS software (ESRI, see Guinet *et al.* 2001).

6.2.3.3 Dietary analysis and prey availability

Faecal samples were collected from the study colony in February 1998, 1999 and 2000. Samples were collected from known individual females where possible and otherwise from areas only frequented by females. Samples were frozen (-20°C) on site and returned to the laboratory for sorting and prey identification. In the laboratory samples were elutriated overnight and subsequently sieved using a 1 mm and 500 μm mesh. Otoliths (sagitta, asteriscus and lapillus) and squid beaks were sorted and identified to species level if possible using the descriptions in Williams and McEldowney (1990) and Reid (1996) and the

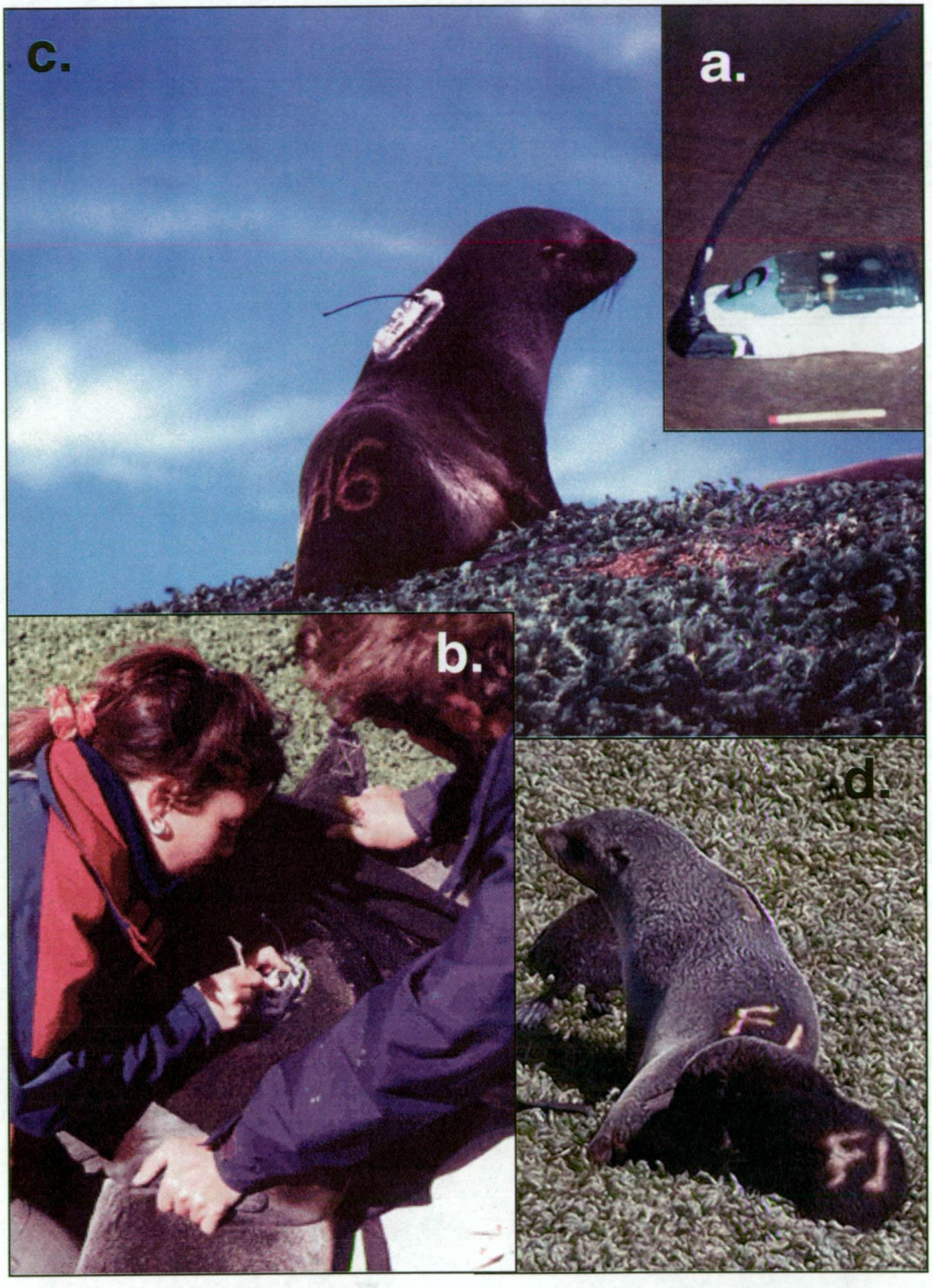


Figure 6.1 (a) PTT/TDR package hydrodynamically shaped to reduce drag (1998 model with Mk5 TDR); *(b)* attaching the PTT/TDR package; *(c)* female seal quipped with PTT/TDR package (1999 model Mk7 TDR); and *(d)* mother and pup post-removal of PTT/TDR package and showing bleach numbers.

reference collection at the CNRS, Chizé, France. Otolith length was measured for those specimens showing little or no sign of erosion. Standard length and mass of fish species were estimated from the conversion of otolith length (mm) using equations (Adams and Klages 1987; Williams and McEldowney 1990; Cherel *et al.* 1997; Olsson and North 1997) for the majority of species. The conversion of lower rostral length to mantle length and squid body mass was achieved using allometric equations from Clarke (1986), Rodhouse *et al.*(1990) and Jackson (1995).

The main prey of Antarctic fur seals at Îles Kerguelen, were mesopelagic myctophids (Chapter 4; Cherel *et al.* 1997), which migrate towards the water surface at night from daytime depths often in excess of 100m (Duhamel *et al.* 2000). Pelagic fish trawls were conducted in the foraging zones determined by concurrent satellite telemetry (see above) of fur seals (Fig. 6.2) in 1998 and 1999 by a 25m research vessel, '*La Curieuse*', from the Institut Français pour la Récherche et la Technologie Polaires (IFRTP). Sampling along transects was conducted at night (2100-0400 hrs) at 50 m depth which approximated the mean dive depth of fur seals recorded in February 1998 (Chapter 2). Five sampling stations, separated by ~0.30° longitude, were located along each transect. Stationary sampling to 150 m (surface, 50 m and 150 m) was also conducted at several sites in 1998 and 1999. This data has been included as it falls within the range of dive depths attained by fur seals during the study (see Chapter 2). Unfortunately due to logistic problems, the full transect was not surveyed in 2000 and was, therefore excluded from analyses. Trawls were carried out using an International Young Gadoid Pelagic Trawl (IGYPT; Duhamel *et al.* 2000; Guinet *et al.* 2001). Samples were collected during 30 min. trawls, travelling at 3 knots travelling along 4 zonal transects separated by 0.40° latitude between 48.20°S, 70.80°E and 49.40°S, 72°00E. Catch per unit effort (CPUE: number of fish caught per hour) was calculated for all fish species sampled in both years. Specimens were identified to species and measured while onboard the ship (standard length and body mass).

6.2.3.4 Maternal body condition

A sample of mothers with pups tagged for longitudinal growth studies (see below), were measured and weighed during shore attendance bouts in February of each of the three seasons. In 1999 and 2000 this included measurements of females equipped with VHF tags for attendance studies to balance yearly sample sizes. Given that no effect on foraging trip duration (FTD) was recorded between seals with PTTs and the observed FTD of 78 control seals in 1998 (Bonadonna *et al.* 2000), I feel that it is reasonable to include these seals in the analyses. In order to compare maternal body condition between years, only females

measured during a common time period (9 February-12 March), were included. As body mass is related to length and, therefore, not necessarily indicative of body condition, we used the body condition index (BCI) used by Guinet *et al.* (1998a) to estimate the relative differences in body mass. Body mass was regressed against standard length by pooling females from all seasons and residual values were calculated. The residual values for each seal, (i.e. the distance above or below the regression line), were compared between years by one-way ANOVA. Those seals for which a positive residual was recorded were heavier than average for animals of that body length.

6.2.4 Maternal allocation and pup provisioning

6.2.4.1 Foraging efficiency

Mass gained by a pup during a foraging cycle (1 foraging trip and subsequent shore bout) has been shown to represent a relatively easily obtainable measure of maternal energy transfer to the pup in several studies (Guinet *et al.* 1999; Georges and Guinet 2000; Guinet *et al.* 2000). The pups of females equipped with PTTs were weighed each day during the fasting period while females were at sea, just before the arrival of the female and again immediately after her departure, to estimate the mass gained by the pup during the foraging cycle (FC). In instances where the body mass was not recorded prior to the arrival of the female, it was estimated by linear regression of pup mass over time during the previous fasting bout.

6.2.4.2 Pup growth rates

A sample of pups were serially weighed and measured (every 6-10 days) to measure growth parameters in each of the three seasons. In 1998, when logistic constraints restricted the duration of the study period, a random sample of 110 pups was selected in early February. In 1999 and 2000 pups were weighed, sexed and marked at, or near, birth (0-1d old) and followed throughout the duration of the lactation period. At approximately one month of age (2 months in 1998), pups were tagged in the trailing edge of each foreflipper (Size 1 Supertags, Dalton Supplies Pty Ltd., UK). Tags were removed at the end of the study. Growth rates in grams per day were calculated individually by the linear regression of pup mass over time for a period common to all three seasons (30 January - 15 March). At the commencement of this period pups were approximately 40-70 days old and many had started to moult. Four to six body mass measurements were collected during the 6 weeks over which growth rates were estimated (1998: n=97; 1999: n=53; 2000: n=91). Sex and year comparisons of mean growth rates conducted on log+1 transformed data by two-way ANOVA. The relationships between growth rates, mean mass and mean length of pups with

mothers fitted with VHF transmitters and maternal length and mean foraging trip duration were tested using linear regression.

6.2.4.3 Pup body condition

The body mass, length and body condition index (BCI, see section 6.2.1.4) of pups during the first week of March were compared by two-way ANOVA to determine any sex and year effects. This time period represented the latest stage during the study at which body mass measurements of pups were comparable between seasons. Residuals were calculated for a regression of pooled pup body mass against standard length.

The body condition of a different sample of pups was also estimated in February 1998, 1999 and 2000 by isotopic dilution of tritiated water (Costa 1987). Pups had been fasting for two days after their mothers had departed to sea, to allow for the complete ingestion of any milk present within the stomach. Pups were subsequently weighed, sexed and measured (standard length). Individual pups were identified from flipper tags as above. Initially a 2 mL blood sample was collected from the caudal gluteal vein to quantify background levels of tritium in the blood. Pups then received a 1 mL injection, administered intramuscularly, of pre-weighed tritiated water (200 μCi *HTO*.ml^{-1}) stored in Wheaton vials (Milleville, New Jersey, USA). After the contents of the vial had been injected, the syringe was rinsed twice with approximately 1 ml of sterile saline and this solution was then injected intramuscularly into the pup. Pups were subsequently held in an enclosure for three hours to allow for isotopic equilibration (Costa 1987; Arnould *et al.* 1996b), after which time an equilibration blood sample (E) was taken to determine total body water (TBW) whereupon the pups were released. The body composition of pups was estimated by calculating TBW using dilution space estimated by the dilution of an hydrogen isotope (HTO) during the three hours. TBW was estimated using the equation in Arnould *et al.* (1996b): TBW (kg) = 0.11 + 0.97*HTO space. Inter-annual and inter-sexual differences in pup body composition were tested using a General Liner Model (GLM) on either arcsine-transformed (proportional) or log-transformed (absolute values) data. All mean values are reported ± 1 SE of the mean unless otherwise stated and statistical analyses were performed using SYSTAT Statistical Software (SPSS Inc. 1998).

6.3 Results

6.3.1 Environmental conditions

Surface chlorophyll plumes of high concentrations were evident to the north-east of the archipelago in 1998 and 2000, but were absent from this region, and dispersed further to the south-east, in 1999. SST surrounding the archipelago was relatively high in 1998 with the surface 5°C isotherm located to the south of the islands. In 1999 and 2000 the position of the

isotherm had migrated further north, in line with the east coast of the Courbet Peninsula (Fig 6.3).

Chlorophyll-a concentration and MCSST values within the foraging range of fur seals (section 6.3.2.1) from the Cap Noir colony were compared between seasons (Fig. 6.4). Elevated levels of Chlorophyll-a (0.292 mg m^{-3}) occurred simultaneously with reduced mean SST (6.4°C) in February 2000, whilst mean SST and chlorophyll-a concentration in 1998 and 1999 were similar, although 1998 was characterised by greater springtime Chlorophyll-*a* levels.

6.3.2 Maternal energy acquisition

6.3.2.1 Foraging distribution

Satellite tracks with concurrent dive profiles were recorded for 32 seals during the three years (Fig. 6.5). Foraging activity was generally distributed within an arc from the northeast around to the south east of the colony. The maximum distance travelled from the colony in February of any year during a foraging trip (68-547 km) was highly, positively correlated with trip duration (r_{28}=0.905, P<0.001; Table 6.1). Females remained within closer proximity of the colony in 1998 (82% <150km) with exception of one female, than in 1999 (75% <150km) or 2000 (22%<150km; Fig. 6.6). The median foraging range of seals in each of the three years was 111, 113 and 215 km respectively.

Marked inter-annual differences are evident in the spatial distribution of diving activity (Fig. 6.5). In 1998, all areas of high diving activity (>0.8 seal hours usage) occurred over the continental shelf break within 100 km of Cap Noir. In 1999 and 2000 the distribution of diving activity was more dispersed. In 1999 areas of highest diving activity again occurred on the margins of the continental shelf to the northeast of the colony, however a second region approximately 300 km to the southeast was also used by the seals. In 2000, a bimodal distribution was evident, with seals foraging further afield over deeper water.

Paired *t*-tests of mean day and night bathymetry per seal indicated no significant difference in the mean depth of water used by seals in either of the three seasons (1998:$t_{10[0.05]}$=1.662, P =0.128 ; 1999: $t_{10[0.05]}$=-1.599, P=0.141; 2000: $t_{9[0.05]}$=-0.729, P =0.485; Fig. 6.7*a*). Overall, the bathymetry of regions visited by seals was also similar between years (ANOVA $F_{2,29}$=0.205, P =0.815; Fig. 6.7*b*), with the mean depth of water being 1160±111 m. In general seals tended to avoid the continental shelf (<500 m), spending the majority of their

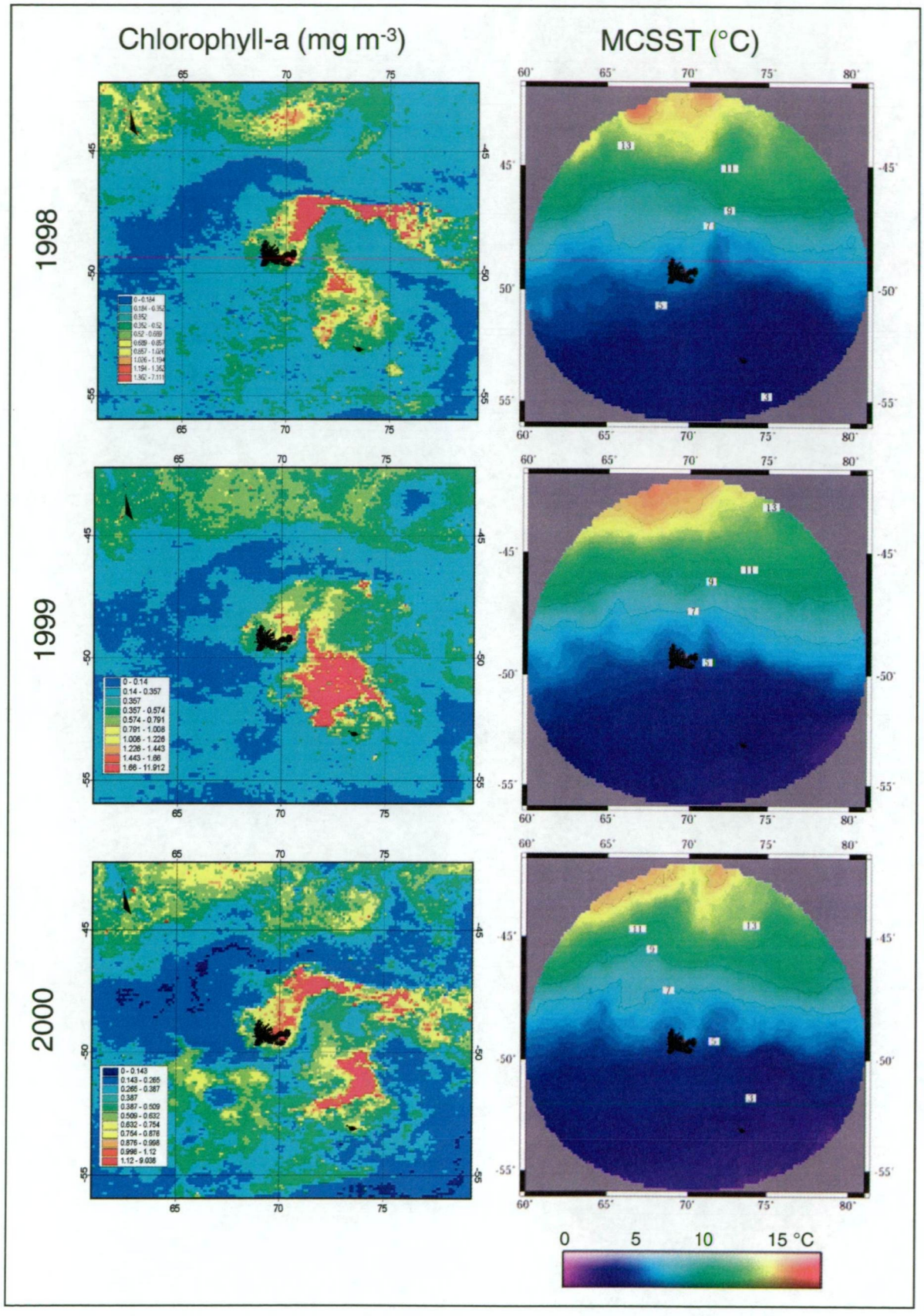


Figure 6.3 Chlorophyll-*a* concentration (mg m^{-3}) and Sea surface temperature (MCSST°C) in the region surrounding the Kerguelen Plateau in February 1998, 1999 and 2000.

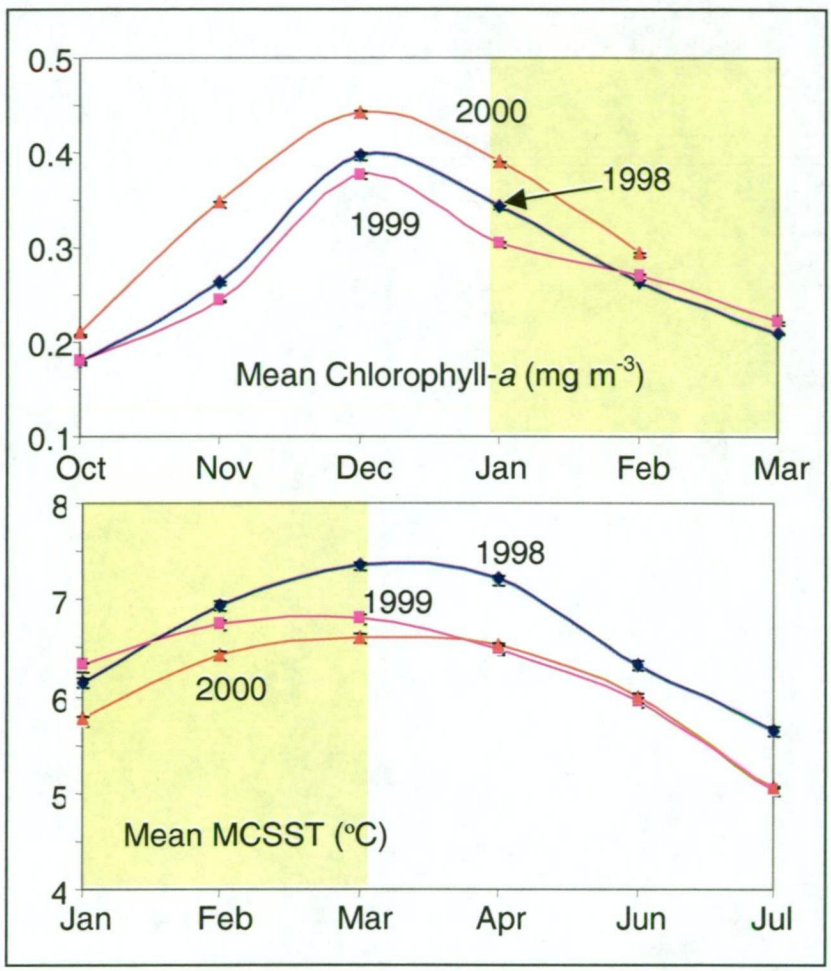


Figure 6.4 Mean Sea Surface Temperatures (°C) and Chlorophyll-*a* concentration (mg m^{-3}) within a 750 km radius of the Cap Noir Antarctic fur seal colony. The study period is shaded in yellow. Bars ± 1 SEM. 750km area=5428 pixels (MCSST) and 22115 pixels (Chlorophyll-a).

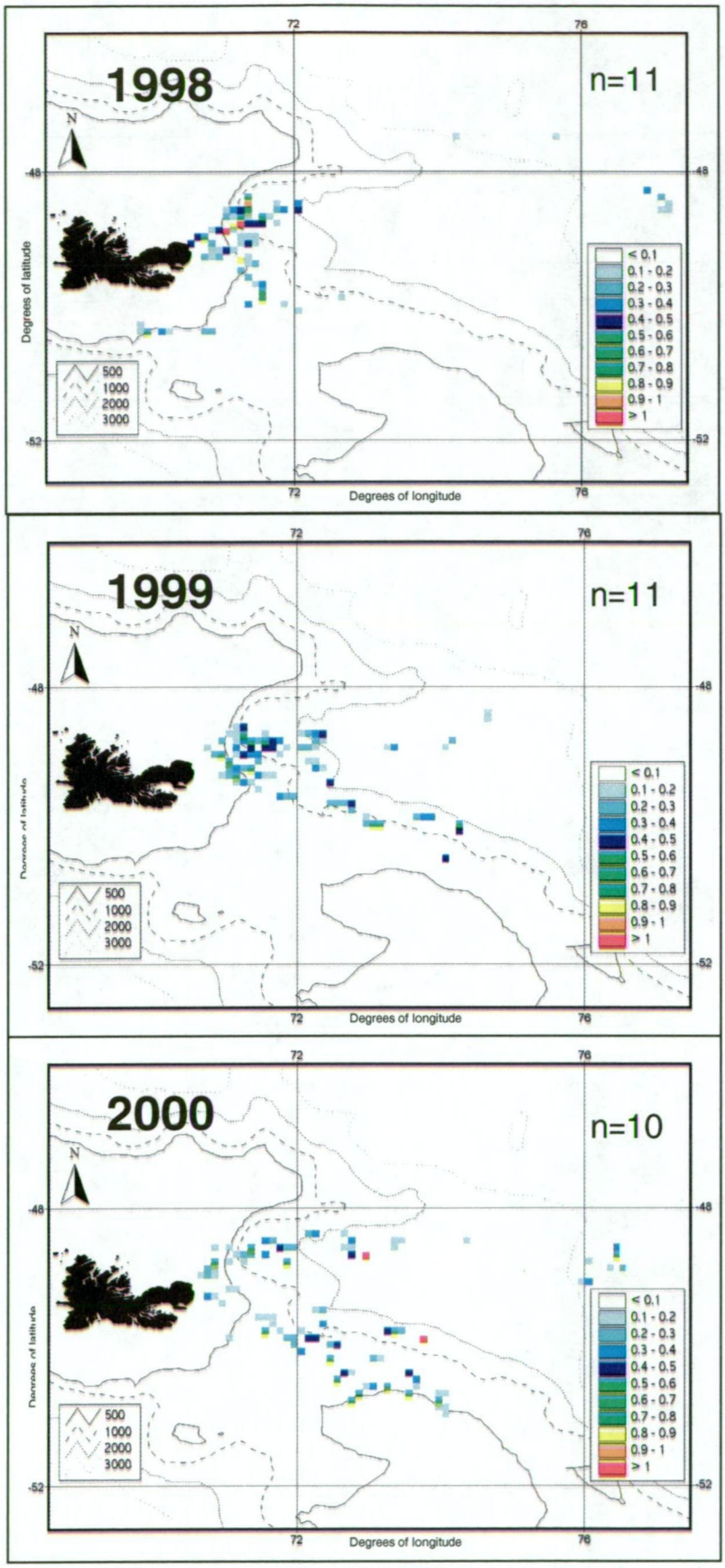


Figure 6.5 Time spent diving (seal hours per 0.1°x0.1° pixel of latitude and longitude) by foraging Antarctic fur seals in 1998, 1999 and 2000. Pixels visited for less than 0.1 seals hours are assumed to be transit regions and are not coloured.

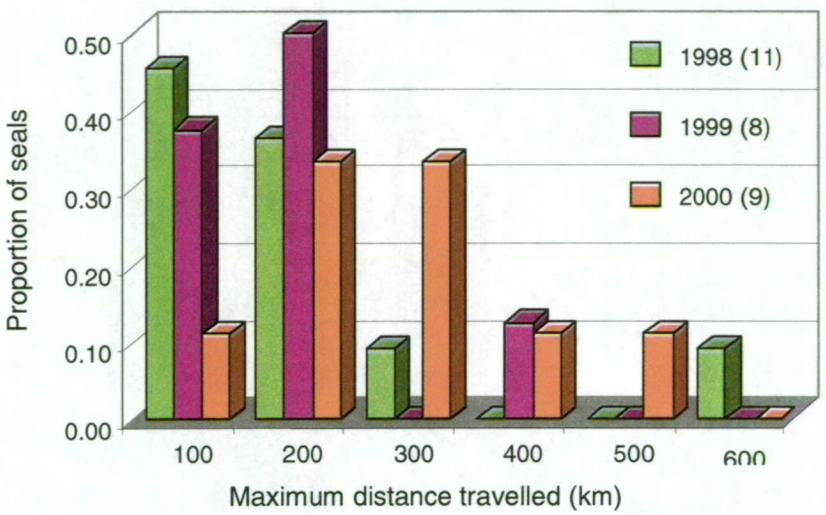


Figure 6.6 Inter-annual variation in maximum distance travelled from the colony (km) during a foraging trip by female seals equipped with satellite transmitters. Sample size in parentheses.

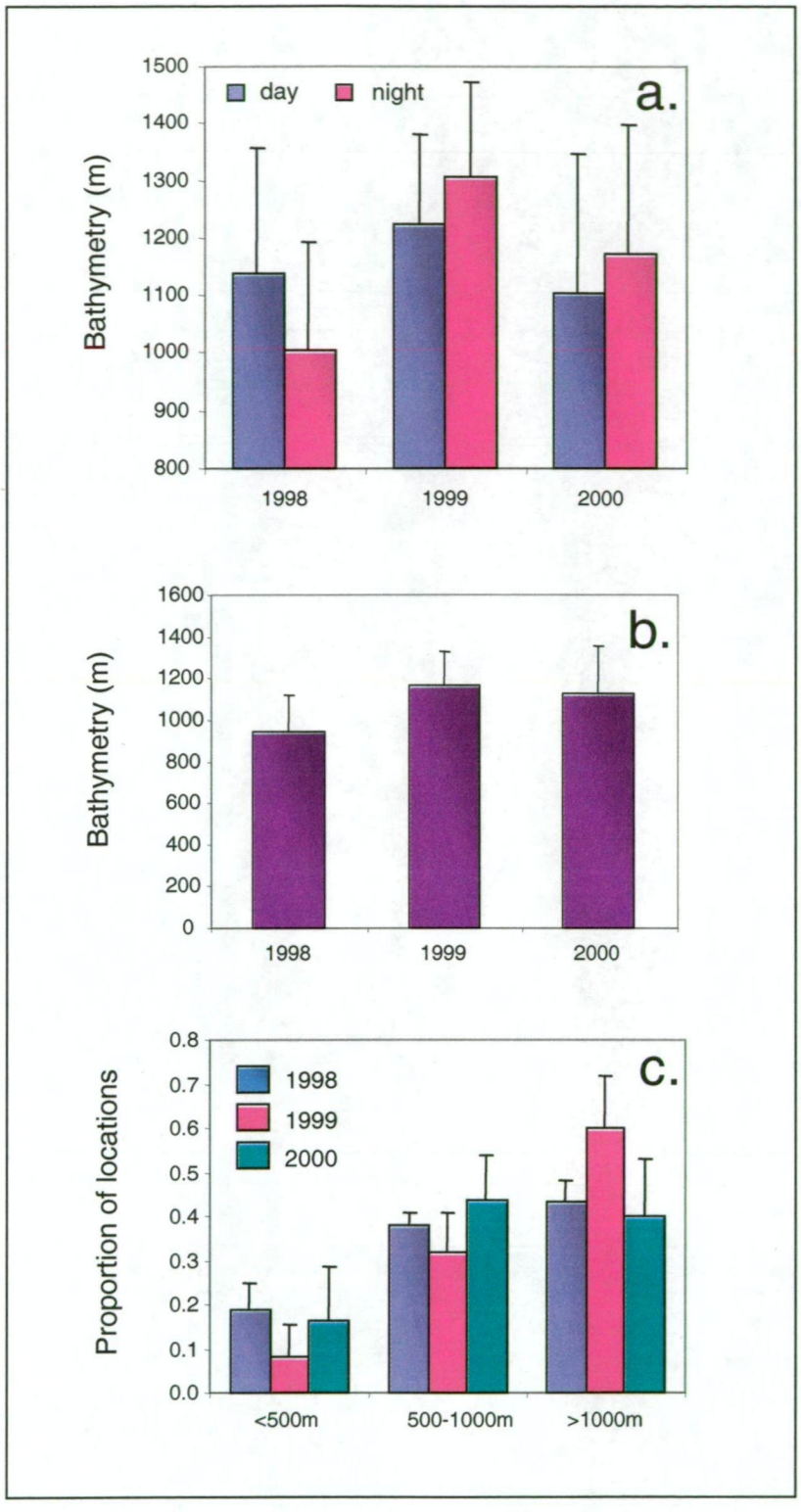


Figure 6.7 (a) A comparison of the day and nighttime bathymetry in regions prospected by Antarctic fur seal females in 1998, 1999 and 2000; (*b)* An inter-annual comparison of mean bathymetry and (*c)* the proportion of PTT locations over continental shelf waters (<500m), continental slope waters (500-1000m) and pelagic waters (>1000m) in 1998, 1999 and 2000.

time over the continental shelf break and pelagic waters (Fig. 6.7*c*). A two-way ANOVA comparing the proportion of locations per seal (arcsine-transformed) between regions (shelf, shelf break or pelagic) and year, confirmed that a significantly higher proportion of locations occurred over the shelf break (38±5 %) and pelagic waters (48±7 %), than over the continental shelf (14±3 % ; $F_{2,87}$=10.756, P <0.001). There were no inter-annual differences or interaction effects.

Table 6.1: Summary statistics for females equipped with TDR/PTT packages in 1998-2000.

Seal	Year	Unit	BDG	Length (cm)	Condition (kg cm^{-1})	FTD (days)	Nightly SST_{TDR} range (ºC)	Range (km)	Pup sex	Absolute PMG (kg)
0	1998	PTT5*	1	117.0	0.232	7.41	4.6-4.9	98	M	2.00
1	1998	PTT5	1	121.0	0.269	5.72	4.6-5.7	97	F	.
2	1998	PTT5*	1	112.0	0.283	8.09	4.2-4.6	152	M	1.65
3	1998	PTT5	1	115.0	0.212	2.96	4.5-4.6	88	M	0.90
42	1998	PTT5*	3	119.5	0.273	16.52	4.6-7.1	547	F	3.60
43	1998	PTT5*	1	117.5	0.260	4.95	4.8	111	F	1.00
47	1998	PTT5*	4	119.0	0.280	8.39	4.2-4.9	243	M	.
51	1998	PTT5	1	119.5	0.295	3.85	4.7-5.4	68	M	.
52	1998	PTT5*	1	112.0	0.262	6.77	4.5-4.7	118	M	1.00
55	1998	PTT5	1	120.5	0.276	6.97	4.4-5.1	145	F	.
57	1998	PTT5	1	126.0	0.273	5.91	4.7-5.1	93	M	1.44
1	1999	PTT7	1	117.8	0.284	7.09	3.8-5.1	190	M	1.24
55	1999	PTT7	1	121.5	0.271	6.45	4.6-6.1	144	F	.
57	1999	PTT7	1	116.1	0.309	4.03	4.5-5.2	98	F	.
L1	1999	PTT7	1	120.3	0.311	4.22	4.1-4.3	86	F	1.58
L2	1999	PTT7	2	115.0	0.292	6.12	4.2-5.2	.	F	2.56
L3	1999	PTT7	2	125.0	0.297	10.03	3.1-4.3	308	M	3.46
L4	1999	PTT7	2	121.5	0.320	4.91	4.4-5.1	123	F	.
L5	1999	PTT7	1	120.0	0.245	7.15	4.2-4.4	.	M	.
L7	1999	PTT7	3	118.3	0.258	15.87	4.6-7.3	.	M	.
L8	1999	PTT7	1	118.5	0.319	4.99	4.8-5.5	103	M	2.24
L9	1999	PTT7	2	115.7	0.270	9.13	4.5-5.4	95	F	.
H3	2000	PTT7	3	114.5	0.304	12.26	3.7-6.5	448	F	3.84
H4	2000	PTT7	1	113.0	0.260	8.91	4.4-5.5	193	M	2.47
H5	2000	PTT7	1	110.0	0.270	6.17	3.9-4.5	186	F	.
H6	2000	PTT7	2	117.0	0.289	9.31	3.5-4.4	259	M	2.94
H7	2000	PTT7	2	115.0	0.246	8.82	3.6-4.2	251	F	2.62
H8	2000	PTT7	1	119.3	0.264	5.16	4.5-4.8	114	M	2.06
S1	2000	PTT7	2	112.0	0.300	9.10	3.9-4.4	215	M	.
S2	2000	PTT7	1	117.3	0.270	3.98	4.6-4.7	.	F	0.65
S3	2000	PTT7	1	117.0	0.265	5.98	4.7-5.1	81	F	1.38
S4	2000	PTT7	2	112.5	0.294	10.37	3.6-5.5	328	F	3.78
Mean	1998			118.1 (1.2)	0.265 (0.007)	7.0 (1.1)	4.2-7.1	160 [111]		1.66 (0.36)
Mean	1999			119.1 (1.9)	0.289 (0.008)	7.3 (1.0)	3.1-6.1	143 [113]		2.22 (0.39)
Mean	2000			114.8 (0.9)	0.276 (0.006)	8.0 (0.8)	3.5-6.5	231 [215]		2.47 (0.39)
Overall				117.4 (0.7)	0.277 (0.004)	7.4 (0.6)	3.1-7.1	178 [134]		2.12 (0.23)

*TDR memory filled prior to end of trip; SE in parentheses; median maximum distance traveled in square brackets

Mean nocturnal SST throughout a foraging trip, as measured by TDR, are plotted by seal for 1998, 1999 and 2000 (Fig. 6.8). In 1998, SST encountered by seals were more homogenous (4-5°C) regardless of whether they foraged north-east or south-east of the colony, in comparison to those in the other two seasons. One exception, seal #42, foraged in an area of warm SST over 500 km to the east of the colony. In 1999 nocturnal SST were more variable within a foraging trip and between seals. A rapid change in SST was apparent post-departure and prior to returning to the colony. In 2000 SST were again variable, however two distinct groups can be observed; those foraging in areas typified by SSTs of 3.5-4.0°C and those in regions averaging 4.5-6.0°C (see Chapter 5). In all three seasons the highest nightly SSTs were recorded by three seals, which travelled in long arcing loops to the north and east of Îles Kerguelen (see Fig. 6.5).

6.3.2.2 Diving behaviour

The diving activities of the 32 seals equipped with satellite transmitters (and TDRs) in February, representing a total of 48 378 dives and 238 days foraging, were assigned to one of four behavioural dive groups (BDG) using 10 dive parameters (see Chapter 2). A significantly greater proportion of seals were assigned to the deep diving BDG1 in 1998 (82%; Fig. 6.9) than in either 1999 or 2000 (55% and 50%, respectively), indicating a greater degree of variability in diving strategies in the latter two years. Seals in BDG1 dived to greater mean depths than other seals and spent a greater proportion of their time at sea diving during generally shorter foraging trips than seals in other BDGs (Table 6.2; Chapter 2). In 1999 and 2000 the proportion of seals assigned to the shallow-active BDG2 increased (36% and 40%, respectively). Six of the dive parameters used to determine the BDG showed considerable inter-annual variation and are summarised in Table 6.2. Mean time spent diving was greater in 1999 than in 2000, whilst the more deeply diving seals in 1998 conducted a significantly greater proportion of their foraging effort at night (97.6%), than seals in other years (81.5-86.9%). Dive frequency in 1998 was lower than other years, being negatively correlated with mean dive depth (PCC r_{32}=-0.771, P<0.001).

The diving behaviour of seals (BDG) was related to SST, maximum distance travelled and bathymetry, with little overlap occurring between groups (Fig. 6.10). Seals assigned to the shallow-less active BDG3 foraged in regions characterised by high mean SST over deep, pelagic water between 400 and 600 km from the colony. The differentiation in habitat use by seals displaying the various dive behaviours is clearly illustrated in two-dimensions (Fig. 6.11). Environmental characteristics of regions used by seals did not vary within a BDG between years, nor between BDG1 and BDG2 in 1999. However the more deeply diving seals in 2000 remained closer to the colony, frequenting warmer waters, than seals in BDG2 (Fig. 6.11).

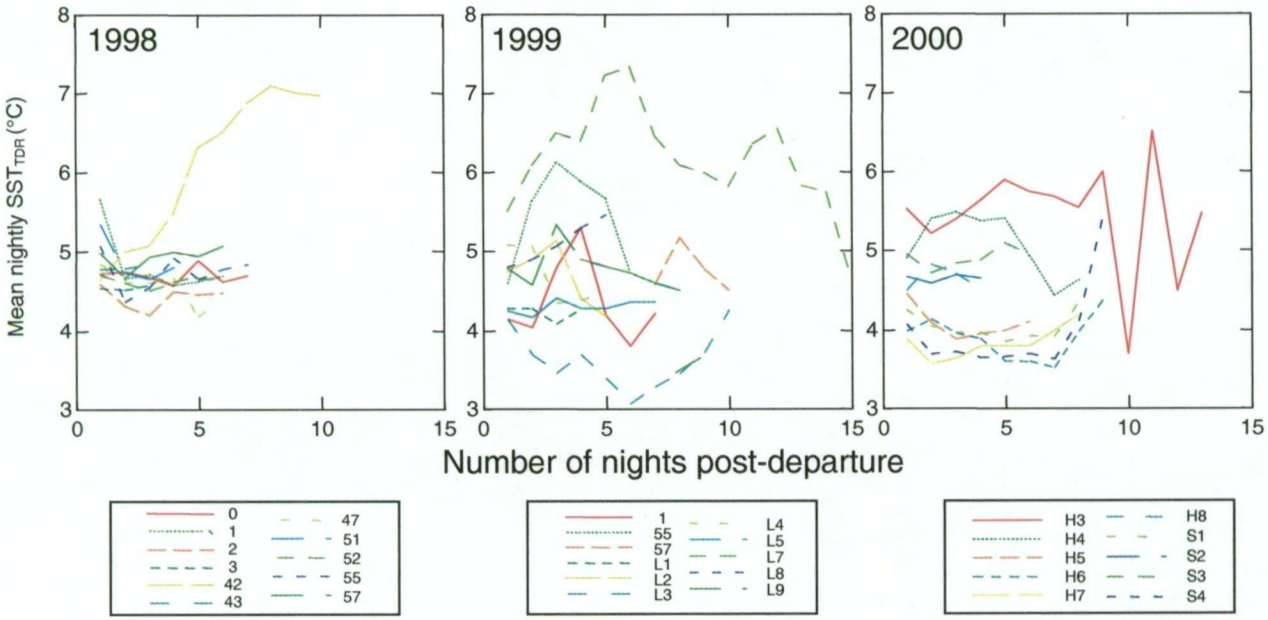


Figure 6.8 Mean nightly sea surface temperatures (SST) during a foraging trip. SST measured by time-depth recorders on female Antarctic fur seals tracked from Cap Noir, in 1998, 1999 and 2000 (legends for seals in boxes).

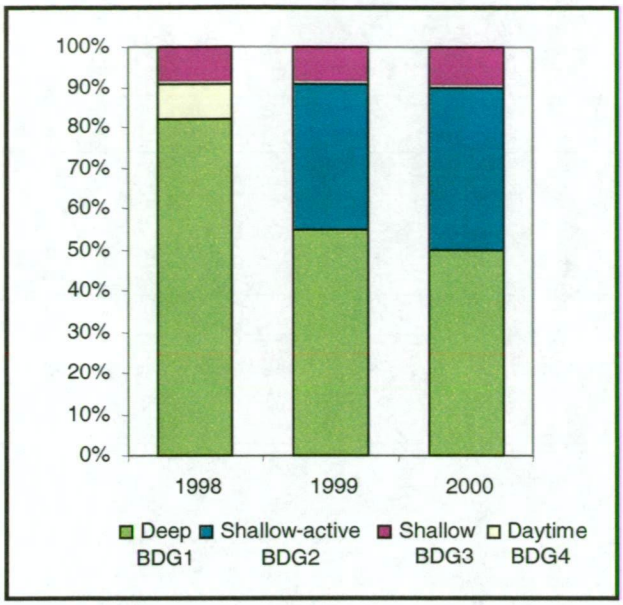


Figure 6.9 The proportion of seals assigned to the behavioural dive categories (BDG).

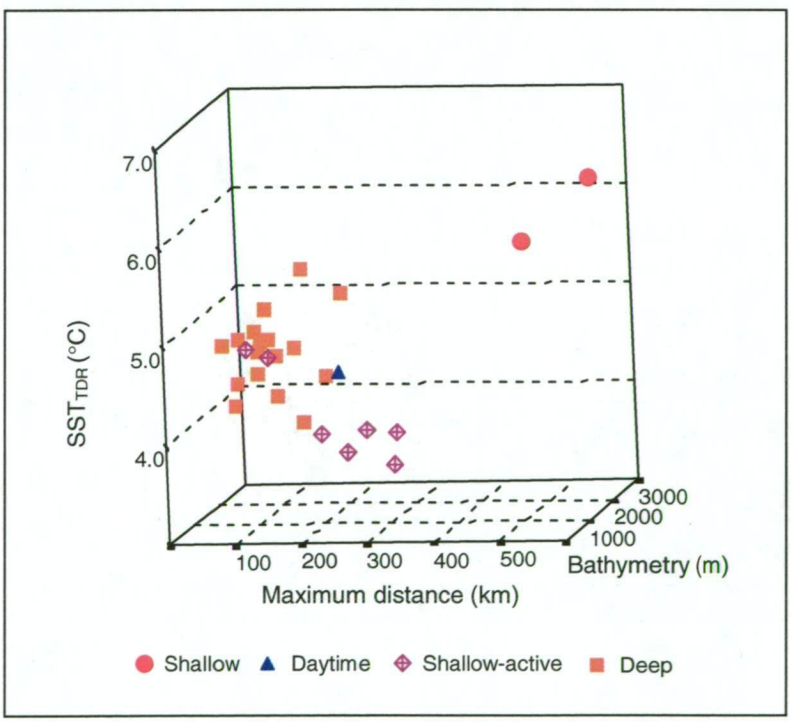


Figure 6.10 The 3-dimensional relationship between the diving behaviour of Antarctic fur seals, environmental paramters (bathymetry and sea surface temperature – SST) and distance travelled from the colony.

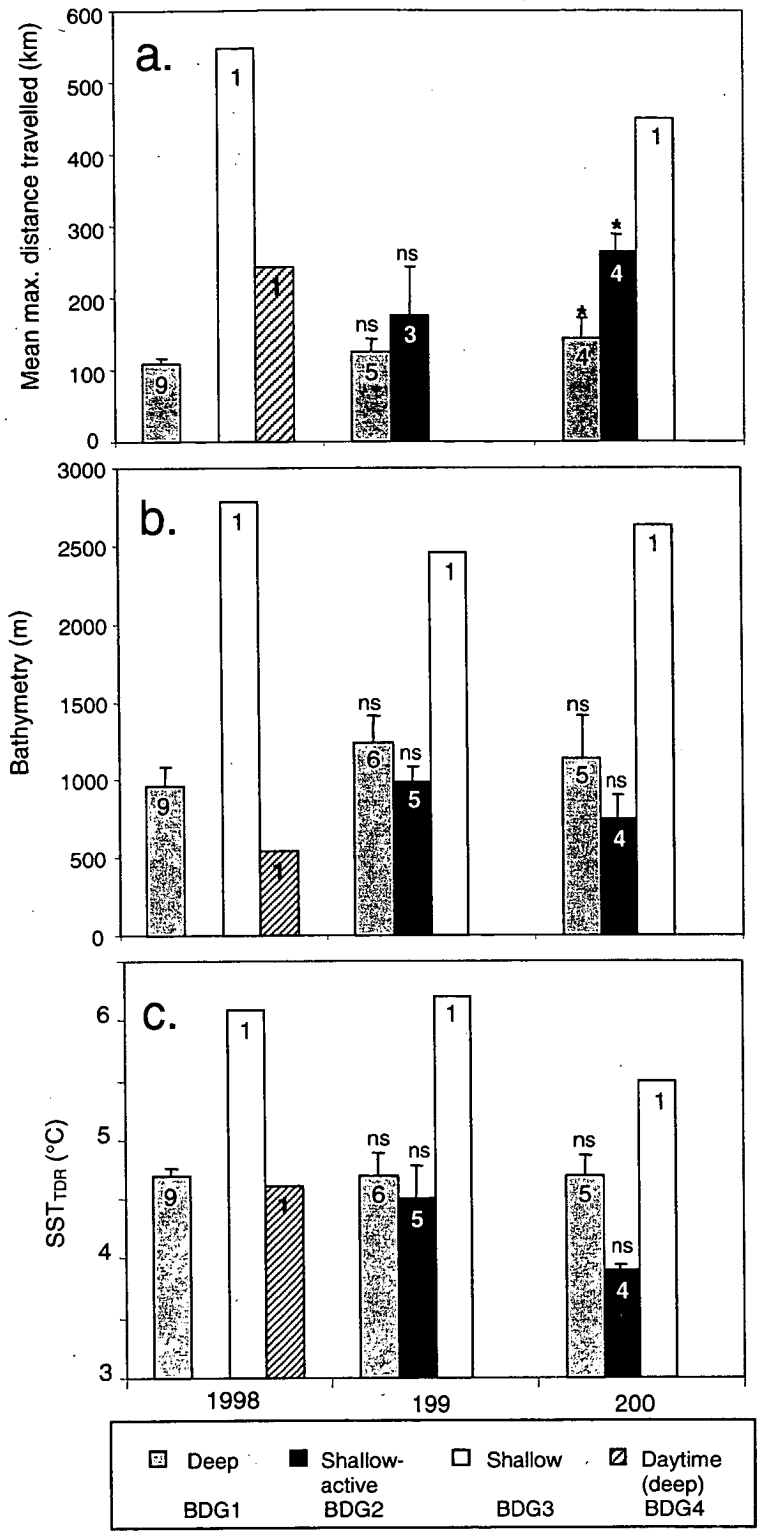


Figure 6.11 (a) Relationship between maximum distance travelled during a foraging trip and behavioural dive group (BDG). Results for between year comparison: BDG1: ANOVA, $F_{2,15}$=1.229, P=0.320; *t*-tests BDG2: (1999 and 2000) : $t_{2.5[0.05]}$=-1.240, P=0.318. Within year comparisons: BDG1&2: 1999 $t_{6[0.05]}$=-0.929, P=0.389; 2000 $t_{6[0.05]}$=-3.308, P<0.05;

(b) Relationship between bathymetry and BDG. Between year comparisons: BDG1: ANOVA, $F_{2,17}$=0.669, P=0.525; *t*-tests BDG 2 (1999 and 2000) : $t_{6[0.05]}$=1.343, P=0.228; Within year comparisons: BDG1&2 1999: $t_{8[0.05]}$=1.053, P=0.323 and 2000: $t_{7[0.05]}$=1.155, P=0.286;

(c) Relationship between SST$_{TDR}$ and BDG. Between year comparisons: BDG1: ANOVA, $F_{2,17}$=0.017, P=0.984; *t*-tests BDG 2 (1999 and 2000) : $t_{6[0.05]}$=1.821, P=0.118; Within year comparisons: BDG1&2 1999: $t_{12[0.05]}$=2.098, P=0.058 and 2000: $t_{11[0.05]}$=1.969, P=0.079.

Table 6.2: Summary of inter-annual variation in five diving parameters estimated for female seals equipped with PTT/TDR units.

	n (*df*)	FTD (d)	Mean max. dive depth (m)	% time spent diving (TSD)*	% of dives at night*	% vertical depth dived at night*	Dive frequency (hr^{-1})
1998							
BDG1	9	5.8 ± 0.6	72.6 ± 4.7	22.5 ± 0.8	98.1 ± 0.4	99.1 ± 0.3	7.2 ± 0.3
BDG3	1	16.5	37	17.7	87.4	85.4	11
BDG4	1	8.4	70	12.7	96.6	96.6	3.9
Mean	11	7.0 ± 1.1	69.1 ± 5.0	21.2 ± 1.2	97.0 ± 1.0	97.6 ± 1.3	7.3 ± 0.6
1999							
BDG1	6	5.6 ± 0.6	68.2 ± 6.4	26.0 ± 1.3	74.6 ± 5.4	64.5 ± 6.3	7.9 ± 0.2
BDG2	4	7.5 ± 1.2	42.3 ± 4.2	25.8 ± 2.2	87.7 ± 1.8	74.7 ± 1.9	11.5 ± 0.7
BDG3	1	15.9	39	15.2	98.5	96.6	8.5
Mean	11	7.3 ± 1.0	56.1 ± 5.5	24.9 ± 1.4	81.5 ± 3.8	71.1 ± 4.5	9.3 ± 0.6
2000							
BDG1	5	6.0 ± 0.8	68.4 ± 9.6	21.6 ± 0.9	80.5 ± 9.8	91.9 ± 3.3	7.3 ± 0.7
BDG2	4	9.4 ± 0.3	36.3 ± 4.2	21.8 ± 1.1	96.3 ± 1.5	93.2 ± 3.6	11.9 ± 1.1
BDG3	1	12.3	32	12.9	81.3	68.6	8.3
Mean	10	8.0 ± 0.8	51.9 ± 7.3	20.8 ± 1.1	86.9 ± 5.3	90.1 ± 3.1	9.2 ± 0.9
Tukey HSD		-	-	99>00	98>99	99<98,00	-
F-ratio	(2,29)	0.247	2.283	3.580	7.335	20.212	2.977
P		0.783	0.120	0.041	0.003	0.00	0.067

* one-way ANOVA performed on arcsine transformed proportions of yearly mean values

6.3.2.3 Attendance patterns

Both the longest mean FTD (13.5 d) and SB (4.2 d) per seal were recorded in 1998 (Table 6.3), while longest absolute FTD (17.7 d) during the study was recorded in 1999. Trip durations of control (VHF) and treatment (PTT) seals were compared by GLM (treatment=fixed and year=random). There was no interaction effect between treatment and year ($F_{2,81}$=1.368, P=0.260), indicating that foraging behaviour of PTT females was similar to that of the control seals and the effect of carrying device packages was minimal. Shore bout ($F_{2,52}$=0.715, P=0.494) and trip duration ($F_{2,52}$=1.951, P=0.152) of VHF females post 19 January did not differ significantly between years when tested using an ANOVA (Table 6.3). However, when the standard error around mean individual FTD (provisioning variability) was compared between years, trip duration was found to be significantly less variable in 2000 than in 1998 or 1999 (one-way ANOVA; $F_{2,49}$=4.612, P<0.05; Fig. 6.12).

Mean shore bout duration per seal expressed as a proportion of the mean foraging cycle (SB+FTD) was compared between years. Shore bout duration constituted on average 19.2±1.3 %; 21.6±0.7 %; 20.4±0.8 % of the foraging cycle in 1998, 1999 and 2000, respectively. No significant differences were detected between years (one-way ANOVA; $F_{2,52}$=1.399, P=0.256).

An increase in FTD throughout the study period was found in 1999 ($F_{1,61}$=13.043, r^2=0.163, p<0.01) and 2000 ($F_{1,150}$=6.360, r^2=0.034, P<0.05), but not in 1998 (Fig. 6.13), which may have been a function of the shorter sampling interval.

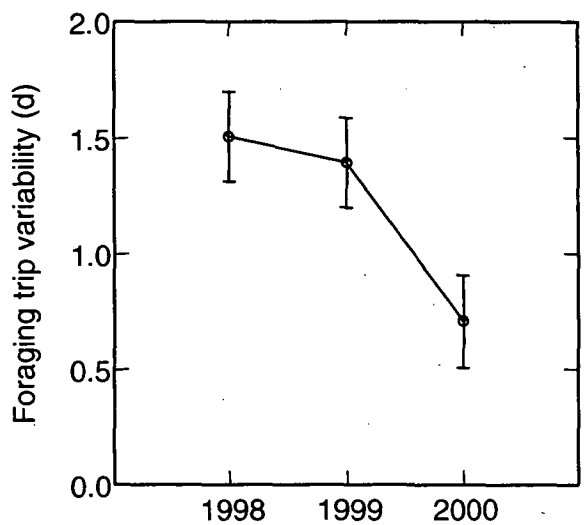


Figure 6.12 An inter-annual comparison of the variability around mean foraging trip duration (SE) for Antarctic fur seal females in 1998, 1999, and 2000.

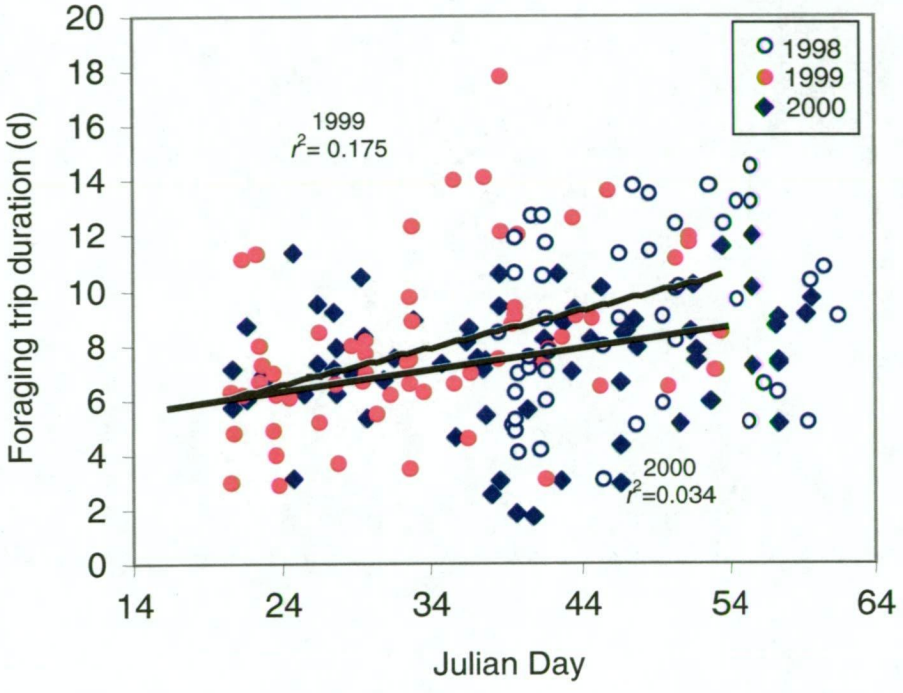


Figure 6.13 Foraging trip duration of lactating Antarctic fur seals during February-March in 1998, 1999 and 2000.

Table 6.3: Foraging trip durations of females equipped with VHF transmitters or PTTs, 1998 - 2000. (Ranges of mean SB and FTD per seal in parentheses).

	Control (VHF)			Treatment (PTT)		
	FTD*	SB[a]	N	FTD**	SB[b]	N
1998	9.3 ± 0.5 (5.5-13.5)[a]	2.2 ± 0.2 (1.0-4.2)	20	7.0 ± 1.1 (3.0-16.5)[b]	2.2 ± 0.3 (0.9-4.6)	11
1999	8.4 ± 0.5 (4.3-12.5)	2.3 ± 0.1 (1.4-3.4)	19	7.3 ± 1.0 (4.0-15.9)	2.3 ± 0.2 (0.9-3.3)	11
2000	7.8 ± 0.5 (4.2-11.1)	2.0 ± 0.1 (1.2-2.9)	16	8.0 ± 0.8 (4.0-12.3)	2.3 ± 0.2 (1.7-3.6)	10
Mean	8.5 ± 0.3	2.2 ± 0.1	55	7.4 ± 0.6	2.2 ± 0.1	32

* represents grand mean of mean value per seal (a – range of means); ** mean of 1FT per seal (b actual trip duration)

The FTD of treatment females was positively correlated to mean bathymetry (PCC r_{32}=0.588, P<0.001), mean SST_{TDR} (PCC r_{32}=0.363, P<0.05) and maximum distance travelled from the colony (see 6.3.2.1) during the course of a foraging trip.

6.3.2.4 Maternal body condition

The length-body mass relationship was plotted for 150 females measured in February 1998-2000 (Fig. 6.14) and was described by the equation:

Body mass (kg)=0.673 x Length-46.957 (r^2=0.583, $F_{1,147}$=209.293, p<0.001),

where length is measured in centimetres. Mean body mass of the seals was significantly higher in 2000 (31.9 kg) than in 1998 (28.6 kg; Table 6.4) when tested by one-way ANOVA, while length was similar between years ($F_{2,147}$=0.315, P=0.315). Residuals calculated from the body mass/length regression served as a body condition index (BCI, see Materials and methods). Seals in 2000 were in significantly better condition than those in both 1998 and 1999 (one-way ANOVA, $F_{1,147}$=10.182, P<0.001).

Table 6.4: Inter-annual comparisons of maternal body condition

	1998	1999	2000	F-ratio	*P*	Tukey HSD
n	62	34	54			
Body mass	28.6 ± 0.6	30.6 ± 0.8	31.9 ± 0.7	7.129	<0.01	98<00
Length	113.8 ± 0.8	115.5 ± 0.7	115.0 ± 0.7	1.165	0.315	-
BCI*	-1.09 ± 0.34	-0.21 ± 0.60	1.41 ± 0.42	10.182	<0.001	98,99<00
Body conditon (kg cm^{-1})[a]	0.250 ± 0.004	0.264 ± 0.006	0.276 ± 0.005	9.775	<0.001	98<00

*body condition index; [a] included for comparisons with other breeding sites

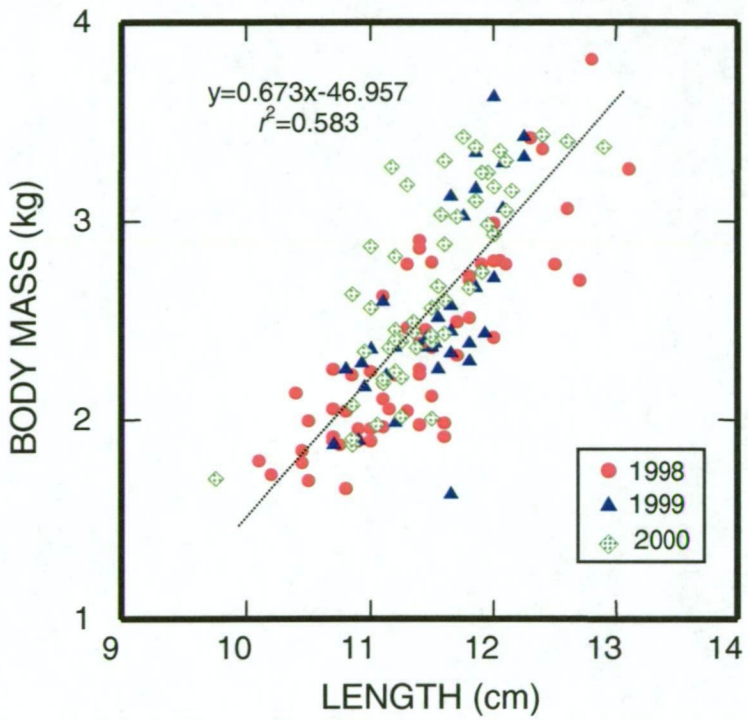


Figure 6.14 Calculation of the maternal body condition index (BCI) from the regression of body mass against length of female Antarctic fur seals.

6.3.2.5 Dietary composition and prey availability

During the three seasons, identifiable prey remains were extracted from 131 scats (1998: n=60; 1999: n=24; 2000: n=47). In 1998, the fish diet of fur seals was more varied with 28 species of fish consumed, compared with 18 species in 1999 and 17 species in 2000. Three species of myctophids (*Gymnoscopelus piabilis*, *G. nicholsi* and *Electrona subaspera*) always constituted the main prey species. However, in 1998 myctophids accounted for only 54% of estimated fish biomass consumption (Fig. 6.15), with species from other fish families, including *Champsocephlaus gunnari*, accounting for 36% of estimated prey biomass consumed. The proportion of myctophids in the diet increased to 74% in 1999 to 82% in 2000.

Prey availability within the seals' foraging zones was assessed in 1998 and 1999. Thirty-two and 36 species of fish were caught at depths of less than 150 m each year, respectively. The catch per unit effort (CPUE; fish per hour) of the three main fish prey species was 2.7-12.3 times higher in 1999 than in 1998 (Table 6.5), although catch-rates of the most common prey species, *G. piabilis,* were always relatively low (0.4-4.9 CPUE) in comparison to those of *G. nicholsi* and *E. subaspera* (3.0 – 32.4 CPUE). Interestingly, catch-rates of myctophids that were not highly abundant within fur seals' diet (Chapter 4), such as *E. antarctica and Krefftichthys anderssoni*, were caught more often than the main prey species. Also, there appears to have been a higher capture-rate of non-myctophid fish species in the trawls in 1998 than in 1999 (Table 6.5), which coincided with an increase in the relative proportion of these fish spp. in the diet of fur seals (Fig. 6.15).

The year of lowest overall prey availability coincided with deeper mean seal dive depths, indicating that higher densities of prey, and/or more energy-rich prey, were possibly located at depths not sampled during trawls. In both years there was a considerable disparity between the abundance of the main prey species within the diet and trawl samples. This could be explained either by prey selectivity of the seals, net avoidance behaviour by the larger prey species, and/or a higher incidence of these particular species at greater depths not sampled during trawls.

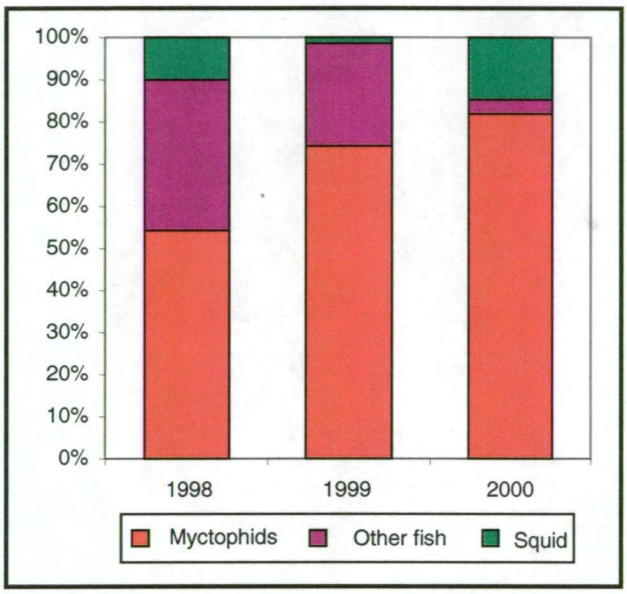


Figure 6.15 The proportion of myctophids, other fish and squid in the estimated prey biomass consumed by Antarctic fur seals in 1998, 1999 and 2000.

Table 6.5: Proportion, standard length and catch per unit effort (CPUE) of fish trawled at less than 150 m depth in fur seal foraging areas in February 1998 and 1999 at 28 stations.

	1998				1999			
	No.	%	SL	CPUE	No.	%	SL	CPUE
Myctophidae								
Gymnoscopelus piabilis	5	0.08	125.8	0.4	69	1.6	124.0	4.9
Electrona subaspera	42	0.7	77.6	3.0	112	2.5	67.0	8.0
Gymnoscopelus nicholsi	135	2.1	46.8	9.6	454	10.2	38.9	32.4
Total - main prey species	182	2.8		13.0	635	14.3		45.3
Electrona antarctica	1348	20.9	50.7	96.3	1115	25.1	41.4	79.6
Electrona carlsbergi					30	0.7	77.6	2.1
Gymnoscopelus fraseri	133	2.1	65.4	9.5	131	2.9	63.6	9.4
Gymnoscopelus braueri	236	3.7	50.6	16.9	144	3.2	50.0	10.2
Gymnoscopelus bolini					8	0.2	204.5	0.6
Gymnoscopelus sp.					1	0.02		0.07
Krefftichthys anderssoni	1085	16.8	44.1	77.5	378	8.5	41.5	27.0
Metelectrona ventralis					2	0.05	56.6	0.1
Protomyctophum tenisoni	1623	25.1	35.4	115.9	1036	23.3	34.7	74.0
Protomyctophum choriodon	10	0.2	68.0	0.7	68	1.5	66.9	4.9
Protomyctophum andriashevi	3	0.05	63.0	0.2	10	0.2	50.2	0.7
Protomyctophum bolini	807	12.5	48.6	57.6	710	16.0	43.6	50.7
Total - other myctophids	5245	81.1		374.6	3633	81.6		259.5
Other fish								
Champsocephalus gunnari	2	0.03	171.9	0.1	3	0.07	77.1	0.2
Other species	1035	16.0		73.9	180	4.0		12.9
TOTAL	6464	100		461.7	4451	100		317.9

6.3.3 Pup provisioning

6.3.3.1 Foraging efficiency

Mass gain per foraging cycle was estimated for 20 mother-pup pairs equipped with PTTs, over the 3 seasons (Table 6.1). The absolute amount of mass gained by the pup was significantly, positively related to foraging trip duration across the three seasons ($F_{1,18}$=34.573, P<0.001, r^2=0.640), but did not vary significantly between seasons ($F_{2,17}$=1.268, P=0.307).

However, the daily rate of mass gain per day of the foraging cycle (PMG) was higher in both 1999 (252±30 g.d^{-1}) and 2000 (234±17 g.d^{-1}) than in 1998 (168±15 g.d^{-1}), when tested by one-way ANOVA ($F_{2,17}$=4.888, P<0.05; Table 6.6).

Table 6.6: Comparisons of pup growth performance, mean body size and provisioning rates between years (one-way ANOVA).

	Sex	1998 (47/50)	1999 (25/28)	2000 (43/48)	df	F-ratio	*P*	Tukey HSD
Mean mass (kg)	M	9.4 ± 0.3	11.6 ± 0.3	11.5 ± 0.3	2,112	20.515	<0.001	98<99,00
	F	8.6 ± 0.2	9.7 ± 0.3	9.6 ± 0.2	2,123	5.75	<0.01	98<99,00
	Pooled	9.0 ± 0.2	10.6 ± 0.3	10.5 ± 0.2	2,238	20.012	<0.001	98<99,00
Mean SL (cm)	M	77.2 ± 0.7	82.2 ± 0.6	81.7 ± 0.6	2,112	18.798	<0.001	98<99,00
	F	74.2 ± 0.6	78.0 ± 0.7	76.9 ± 0.5	2,123	10.264	<0.001	98<99,00
	Pooled	75.7 ± 0.5	80.0 ± 0.5	79.1 ± 0.5	2,238	21.918	<0.001	98<99,00
Growth rate (g.d^{-1})	M	7 ± 6	10 ± 12	77 ± 7	2,112	26.899	<0.001	98,99<00
	F	1 ± 7	18 ± 12	56 ± 6	2,123	14.381	<0.001	98,99<00
	Pooled	4 ± 5	14 ± 8	66 ± 5	2,238	38.703	<0.001	98,99<00
		(-164-127)*	(-111-168)	(-28-166)				
PMG (g.d^{-1})**	Pooled	168 ± 15 (7)***	252 ± 30 (5)	234 ± 17 (8)	2,17	4.882	<0.05	98<99,00

* range of growth rates; ** calculated per day of foraging cycle; ***sample size in parentheses (M/F)

6.3.3.2 Growth rates

Pup body length was shorter in 1998 than in 1999 and 2000 (ANOVA, 28.611, P<0.001), and male pups were, on average, longer than female pups ($F_{1,235}$=58.853, P<0.001), with no interaction effect recorded between sex of the pup and year ($F_{2,235}$=1.270, P=0.283). Mean body mass also varied in relation to both year ($F_{2,235}$=3.746, P<0.001) and pup sex ($F_{1,235}$=129.5, P<0.001) with a significant interaction effect ($F_{2,235}$=25.379, P<0.05; Table 6.6).

Mean rates of pup growth in February/March ranged from negligible rates in 1998 (4±5 g.d^{-1}) up to 66±5 g.d^{-1} in 2000, with rates as high as 168 g d^{-1} measured for one pup in 1999. Mean growth rates were significantly higher in 2000 than in either 1998 or 1999 (see Table 6.6; Fig. 6.14), and were unrelated to pup sex (two-way ANOVA, $F_{2,235}$=0.834, P=0.362).

Maternal characteristics (trip length and trip duration) of seals fitted with VHF transmitters were related to various pup parameters such as the rate of growth, and mean body mass and body length in each of the three seasons (Fig. 6.16). Mean FTD was significantly, positively related to the mean body mass of pups during the study period only in 1999 ($F_{1,16}$=5.653, P<0.05; r^2=0.215) and was not related to growth rates of the pups in any year. Similarly, the regularity of FTD (i.e. SE, see section *6.3.2.3*) was negatively related pup growth rates and mean body mass

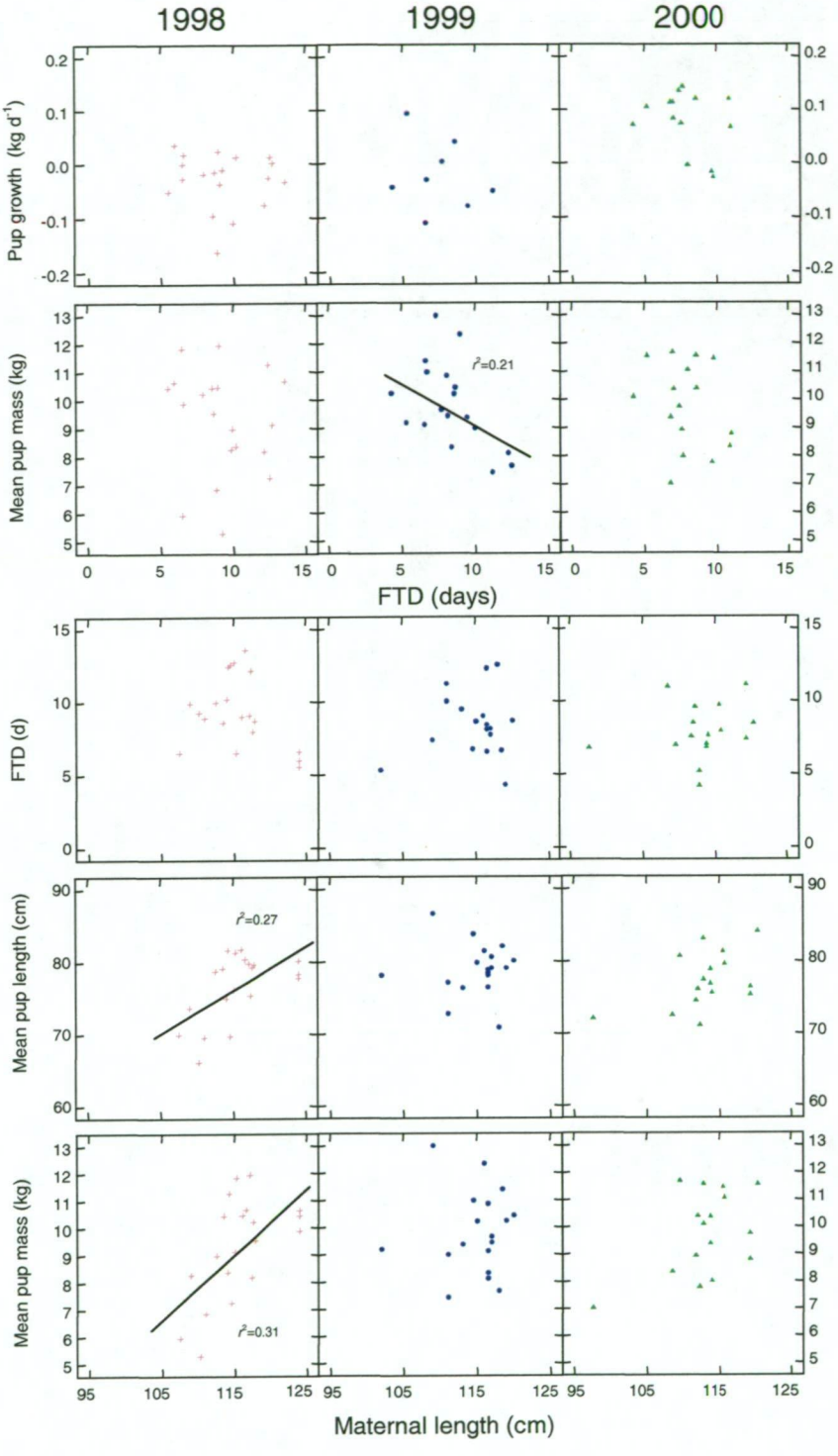


Figure 6.16 Relationships between maternal (foraging trip duration and length) and pup parameters (growth rates, mean mass and length).

only in 1999 ($F_{1,6}$= 6.982, r^2=0.461, P<0.05 and $F_{1,15}$=10.130, r^2=0.363, P<0.01, respectively). In addition, higher mean body masses and lengths of pups were positively related to maternal size in 1998, ($F_{1,18}$=8.024, P<0.05, r^2=0.270 and $F_{1,18}$=5.653, P<0.01, r^2=0.312, respectively) but not in 1999 or 2000.

6.3.3.3 Pup body condition

Body mass was significantly, positively related to the length of pups ($F_{1,186}$=482.796, P <0.001; r^2=0.720; Fig. 6.17). Length and body mass of the pups varied in relation to pup sex ($F_{1,182}$=34.67, P<0.001 and $F_{1,182}$=20.53, P<0.001, respectively) and year (see Table 6.7) with no interaction effects. The body condition index (BCI) however varied between years (Table 6.7) but not in relation to pup sex ($F_{1,182}$=0.802, P=0.372). Interestingly, the length of female pups was similar between years whilst male pups were significantly longer in both 1999 and 2000 than in 1998. Body mass and BCI were always higher in 2000 than in 1998 for both male and female pups, with measurements in 1999 often being intermediate.

Table 6.7: The body mass, standard length and body condition index of pups in early March 1998, 1999 and 2000. Statistical results from one-way ANOVA with year as the factor.

Parameter	Sex	1998 (24/29)^	1999 (52/40)	2000 (21/22)	*df*	*F*-ratio	*P*
Body mass	M	$9.7 \pm 0.5^{a,b}$	$11.4 \pm 0.3^{a,c}$	$13.0 \pm 0.6^{b,c}$	2,94	10.89	0.000
(kg)	F	9.1 ± 0.4^{a}	10.1 ± 0.3	10.6 ± 0.3^{a}	2,88	4.41	0.019
	Pooled	$9.4 \pm 0.3^{a,b}$	10.8 ± 0.2^{a}	11.8 ± 0.4^{b}	2,185	13.78	0.000
Body	M	$80.4 \pm 1.0^{a,b}$	83.5 ± 0.5^{a}	83.9 ± 1.1^{b}	2,94	4.91	0.009
Length (cm)	F	78.2 ± 0.8	79.1 ± 0.6	79.0 ± 0.7	2,88	0.43	n.s
	Pooled	79.2 ± 0.7^{a}	81.6 ± 0.5^{a}	81.4 ± 0.8	2,185	4.79	0.000
BCI	M	-0.69 ± 0.25^{a}	-0.33 ± 0.17^{b}	$1.06 \pm 0.28^{a,b}$	2,94	12.73	0.000
	F	-0.40 ± 0.20^{a}	0.18 ± 0.15	0.73 ± 0.24^{a}	2,88	7.38	0.001
	Pooled	-0.53 ± 0.16^{a}	-0.11 ± 0.12^{b}	$0.89 \pm 0.18^{a,b}$	2,185	18.53	0.000

a-c represent within line differences in mean values between years (Tukey HSD); ^sample sizes of male and female pups in parentheses.

The body condition, of 71 pups, was also assessed by isotopic dilution over the three seasons (Table 6.8). Absolute TBW was significantly related to body mass in all three seasons (Fig. 6.18), and in 1999 the relationship between body mass and TBW differed significantly between the sexes (ANCOVA, mass: $F_{1,27}$=208.02, P<0.001; sex: $F_{1,27}$=17.19, P<0.001; Fig. 6.18). Consequently, year and sex comparisons of absolute TBW were made using a General Linear Model, with mass as a covariate. Absolute TBW differed in relation to sex and year (GLM, Sex: $F_{1,5}$=25.138, P<0.01; Year: $F_{2,7.8}$=6.035, P<0.05) with no interaction effect. A comparison of the estimated marginal means (Table 6.8), indicates that male pups had significantly higher

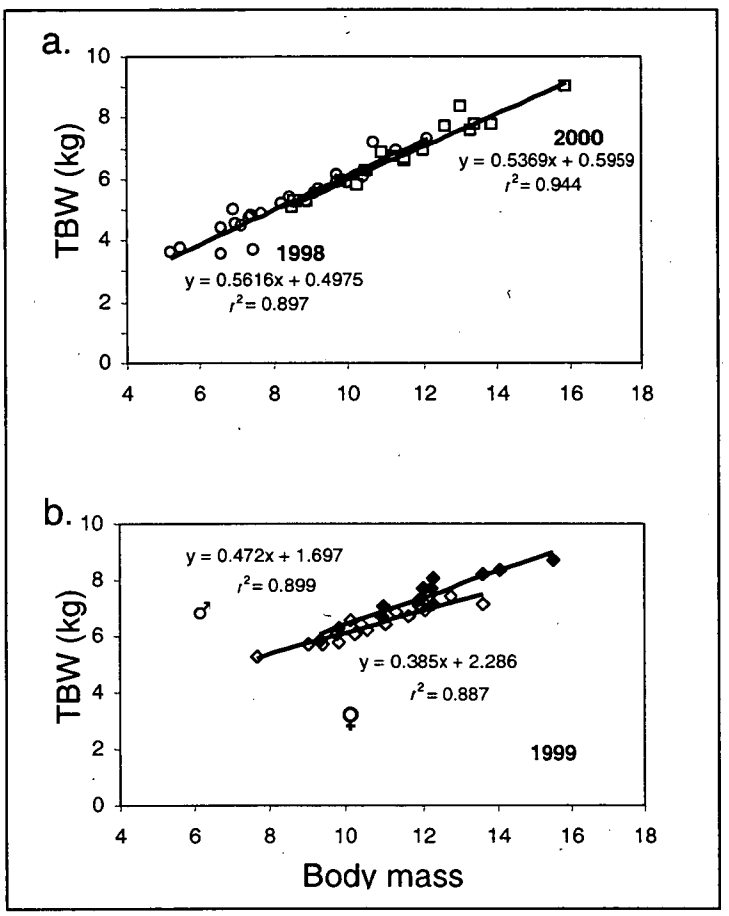


Figure 6.17 (a-b) The relationship between the body mass (kg) and total body water (TBW) of Antarctic fur seal pups in (*a*)1998 (open circles) and 2000 (filled squares); (*b*) a comparison of the TBW/body mass slopes for male (filled diamonds) and female (open diamonds) pups, which differed significantly in 1999 (see text).

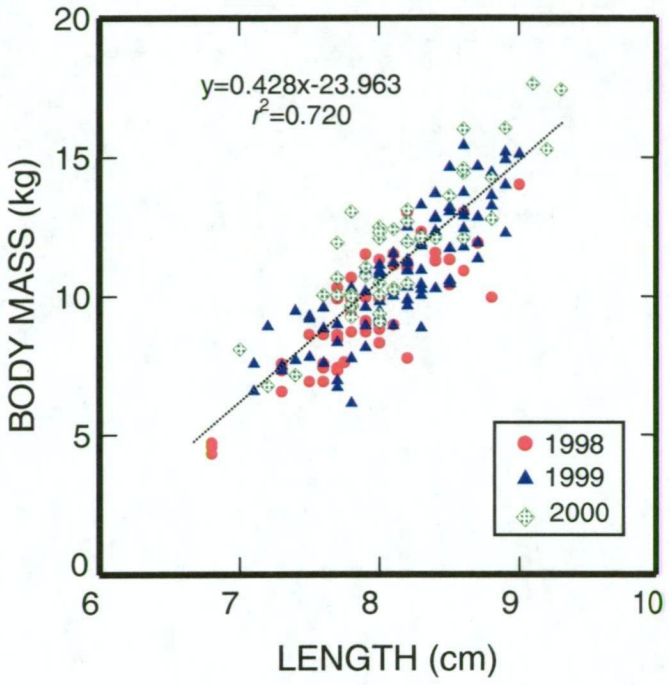


Figure 6.18 Regression relationship between body mass and body length of Antarctic fur seal pups at Îles Kerguelen in 1998, 1999 and 2000.

levels of TBW on a kilogram for kilogram basis, i.e. male pups had more lean body mass than female pups.

Both male and female pups weighed less and had significantly lower absolute levels of TBW in 1998 than in 1999 and 2000 (Table 6.8). Proportional TBW and total body lipid (TBL) were unrelated to pup sex but were, however, significantly lower in 1998 than in 2000, indicating that pups were in poorer condition in 1998.

Table 6.8: Inter-annual comparison body condition parameters for male and female pups as estimated by isotopic dilution (sample sizes of male and female pups in parentheses).

	1998 23 (11/12)	1999 30 (14/16)	2000 18 (11/7)	*df*	*F*-ratio	*P*
Body mass (kg)						
Males	$8.4 \pm 0.5^{a,b}$	12.1 ± 0.4^{a}	13.0 ± 0.6^{b}	2,29	24.65	<0.001
Females	$8.3 \pm 0.6^{a,b}$	10.7 ± 0.4^{a}	10.5 ± 0.5^{b}	2,36	8.49	<0.001
TBW (kg)						
Males	$5.3 \pm 0.3^{a,b}$	7.4 ± 0.2^{a}	7.6 ± 0.3^{b}	2,29	19.74	<0.001
Females	$5.1 \pm 0.3^{a,b}$	6.4 ± 0.2^{a}	6.2 ± 0.3^{b}	2,36	9.89	<0.001
EMM TBW (kg)						
Males	6.3 ± 0.1	6.6 ± 0.1	6.4 ± 0.1			
Females	6.1 ± 0.1	6.3 ± 0.1	6.2 ± 0.1			
TBW (%)	62.4 ± 1.0^{a}	60.8 ± 0.6	59.0 ± 0.5^{a}	2,65	4.62	<0.05
TBL (%)	13.9 ± 0.9^{a}	15.3 ± 0.5	16.8 ± 0.5^{a}	2,65	4.24	<0.05

a,b represent significant within line differences between yearly means as indicated by Tukey HSD post-hoc test
EMM = estimated marginal means

6.4 Discussion

For most groups of mammals, such as otariids, the responsibility of parental care lies solely with the mother and is largely determined by her ability to efficiently locate prey during the lactation period (Bonner 1984). Under favourable environmental conditions with abundant food resources, an increase in the rate of offspring provisioning is associated with an increase in offspring growth rates (e.g. Serengeti spotted hyaenas, *Crocuta crocuta,* Hofer and East 1993). At nutritional independence, mammalian offspring, and pinnipeds in particular, have a finite period of time in which to learn how to forage for themselves before exhausting their energy reserves. Consequently, offspring size and body condition, particularly fat levels at this critical time could influence survival (Baker and Fowler 1992; Lunn *et al.* 1993). Environmental conditions have also been shown to affect juvenile survivability in northern fur seals (York 1995). Thus, optimization of maternal foraging efficiency, during periods of reduced prey availability and climatic variability, could potentially influence offspring survival and future reproductive success.

This three-year study of a myctophid predator-prey ecosystem has demonstrated that many parameters relating to otariid foraging behaviour, such as the location of feeding zones, diving activity and diet, varied concurrently with changing oceanographic conditions and food availability in the Polar Frontal Zone at Îles Kerguelen (Table 6.9). The body condition of both mothers and pups also varied between years, and were lowest in the year of higher local sea surface temperatures. Pup growth rates during the study period (February-March) were negligible in this year (1997/98), one of the strongest El Niño events on record (Grotzner *et al.* 2000). However, the large-scale breeding failures which have been reported at other Antarctic fur seal breeding sites affected by climatic anomalies (Trillmich and Dellinger 1991), for example Bird Island, where seals depend on krill, *Euphausia superba* (Croxall *et al.* 1988; Boyd *et al.* 1995), were not observed at Îles Kerguelen. Instead, female seals seemed capable not only of locating prey in 1998, albeit regularly at considerable depths and greater effort, but they were also able to maintain the provisioning of their pups through the latter part of the lactation period. In this discussion the linkages between the various aspects of maternal acquisition of prey resources and the transfer of energy to the pups are explored in relation to the observed variability in environmental conditions surrounding the Kerguelen Archipelago in 1998, 1999 and 2000.

Table 6.9: Inter-annual comparison of environmental, maternal acquisition and allocation parameters

Parameter		Class.^	1998	1999	2000
Environment					
Mean MCSST (°C)		750km	6.9	6.7	6.4
TDR nightly SST (°C)		PTT	4.8	4.8	4.5
Mean Chlorophyll-*a* (mg m^{-3})		750km	0.263	0.269	0.292
Bathymetry (m)		PTT	1088	1257	1130
Maternal acquisition					
Median Max distance from colony (km)		PTT	111	113	215
Proportion deep divers (BDG1)		PTT	82%	55%	50%
Body condition index		Pop.	-1.09[a]	-0.21[b]	1.37[a,b]
Trip duration (days)		VHF	9.3	8.4	7.8
Diet					
Proportion myctophids (%)		Pop.	54	74	82
No. fish taxa consumed		Pop.	28	18	17
Prey availability					
Catch per unit effort of primary prey*			Low	High	-
Pup allocation					
Body condition – TBW%		Pop.	Low	Int.	High
- BCI	M	Pop.	Low	Low	High
	F	Pop.	Low	Int.	High
Mean March body mass (kg)		Pop.	Low	Int.	High
Growth rates (30-65 J days) g d^{-1}		Pop.	Zero	Low	High
Milk fat (mean % lipid)		Pop.	-	43.3%	53.2%

^ classification; Pop. = population measure; * *Gymnoscopelus nicholsi, G. piabilis* and *Electrona subaspera.*

6.4.1 Variability in environmental conditions and prey availability

It is clear from the findings of this study, in addition to results presented by Guinet *et al.* (2001) that environmental conditions including sea surface temperature and chlorophyll-a concentration varied considerably within the foraging range of Antarctic fur seals between years. The warm SST anomaly recorded in the Kerguelen region for 1997/98 (Fig. 6.19) represented the largest warm episodic event in recent years, and coincided with a large ENSO in the central Pacific Ocean. Warm SST occur in the Kerguelen region within one year and 4.2 to 5.4 years after an El Niño and have been correlated with depressed breeding performance and body condition in blue petrels (*Halobaena caerulea*) nesting at the Kerguelen Archipelago (Guinet *et al.* 1998b). Francis *et al.* (1998) have linked anomalous, warm SST to the occurrence of longer foraging trips in Juan Fernandez fur seals, while warm SST in March at Macquarie Island in the Southern Ocean have been associated with decreased fecundity of Antarctic fur seals the following year (Goldsworthy, unpublished data). The body condition of Antarctic fur seal females at Cap Noir was particularly poor in 1998 following a year of sustained anomalously high temperatures. As the ecology of fur seals breeding at Îles Kerguelen had not previously been studied, it is unclear whether the poor maternal body condition witnessed in 1998 reflected (*a*) environmental conditions during that particular breeding season, (*b*) a combination of several years of anomalous conditions, or (*c*) a combination of both winter and summer feeding conditions.

Prey availability (as measured by CPUE of myctophids in the fur seals foraging zone) was increase by 200-700% from 1998 to 1999 for the three main prey species. The spatial distribution of seals in 1998, was correlated with the highest availability of fish prey (Guinet *et al.* 2001) located approximately 60-70 km from the colony. The abundance, size and species composition of fish caught in nets, however, did not generally reflect those identified from seal scats over the same time period. The mean size of *Gymnoscopelus piabilis* consumed by seals in 1998 and 1999 (124-130 mm; Chapter 4) was similar to those caught in net trawls (125-126 mm), however the proportional abundance of this species in the net (<1 %) was considerably lower than its occurrence, in terms of biomass, in the diet of seals (27-28 %; Chapter 4). This disparity may be explained by efficient net avoidance behaviour on the part of *Gymnoscopelus piabilis*, one of the larger species of myctophid. Alternatively, a higher occurrence of this species may have occurred at depths greater than the 50m generally sampled during trawls. Given the high-energy value of *G. piabilis* (Chapter 4), these were expected to be a highly-preferred prey item, selectively foraged by seals. The sizes of the other main prey species, *G. nicholsi* and *E. subaspera* which were also relatively lipid rich per gram of body mass, were considerably larger (150-215%) in scat samples than in net trawls, confirming the above hypotheses. *Electrona subaspera,* which form the main prey component of Antarctic fur seals at Macquarie Island, were larger (91-94 mm) than those taken in this study (78-83 mm), at Île de

Croy, Kerguelen (71 mm; Cherel *et al.* 1997) and those captured in nets (41-51mm). Thus, it is possible that the largest available species of myctophids are the preferred prey of Antarctic fur seals at any of the breeding sites where myctophids constitute the majority of the diet.

Inter-annual variability was also reflected in the between year dietary preferences of seals with the number of prey species taken being more variable in the year of lower overall prey abundance (1998) than in 2000. *Champsocephalus gunnari*, the commercially-caught mackerel icefish, formed a considerable component of the diet in 1998 (13% of prey biomass, Chapter 4), which appears to have been exceptional, as it was absent from scats collected in 1999 and 2000, although it was available to seals (Chapter 4; Claudet 2001). Although no capture data are available for 2000, I have assumed this to be a year of high food availability given the higher body condition index recorded for lactating females in this year. A direct correlation between body condition and prey availability and/or environmental factors, such as sea surface temperature, has previously been observed for several species of marine mammal, including Galapagos fur seals (*Arctocephalus galapagoensis;* Trillmich and Kooyman 2001), Minke whales (*Balaenoptera acutorostrata*; Ichii *et al.* 1998) and Fin whales (*B. physalus;* Lockyer 1986). The greater importance of the energy-rich species, *Gymnoscopelus nicholsi* and *G. piabilis,* in the diet of fur seals in 2000 (Chapters 3 and 4) may have contributed to the higher body condition index observed during this year.

6.4.2 Maternal acquisition strategies and environmental variability

The spatial distribution and diving activity of seals clearly differed during years of changing prey availability. Individual variation in the way seals responded to their altered environment, however, accounted for much of the variability in diving behaviour. One common measure of foraging effort often recorded in fur seals populations is foraging trip duration (Costa *et al.* 1989; Costa *et al.* 1991; Heath *et al.* 1991; Francis *et al.* 1998; McCafferty *et al.* 1998; Georges and Guinet 2000). Yet at Cap Noir, despite considerable inter-annual fluctuations in marine productivity, no significant increase in trip duration was observed. Trip duration was correlated with mean nightly SST and bathymetry, and over the three seasons was positively correlated with increasing maximum distance travelled from the colony as is common with central place foragers (Boyd 1999; Robinson 2002). As distance travelled from the colony was greater in years of improved food availability, no direct relationship between food abundance and trip duration was evident between years. Instead, the inter-annual difference lay in the individual variability associated with mean trip duration. Seals that made longer foraging trips, on average, displayed a higher degree of variability in trip duration. It was apparent that seals in 2000 made foraging trips more consistent in duration than seals in 1998 and 1999. Trips of longer duration interspersed with shorter trips might be expected for females trying to improve their body condition. This has been proposed for Antarctic fur seals at Macquarie Island that conduct both

overnight and extended foraging trips (Goldsworthy 1999) and for several species of pelagic seabirds (Chaurand and Weimerskirch 1994; Weimerskirch *et al.* 1994; Weimerskirch 1998). Hence, the higher variability in mean individual trip duration in 1998 and 1999 may be indicative of a similar strategy at Cap Noir.

Conversely, however, the level of inter-individual variability in diving strategies was reduced under conditions of lower prey availability. Seals studied in 1998 tended to remain within closer proximity to the colony than in other years, diving to greater mean depths over the plateau edge. We can only assume that the degree of intra-specific competition, with the majority of seals foraging in the one region (Bonadonna *et al.* 2000), was minimised by physiological differences in an individual's diving capabilities. Caldow *et al.* (1999) stated that individual variability in the competitive ability of foraging animals arises from variation in an individual's foraging efficiency and their susceptibility to interference, i.e. how an individual copes in increasing densities of competitors. The foraging behaviour of the sample of seals studied in 1998, 1999 and 2000 indicates that in years of reduced prey availability there were advantages, or perhaps reduced costs, associated with remaining closer to the colony, even at the risk of higher levels of intra-specific competition. The availability of prey locally undoubtedly influenced the three-dimensional distribution of seals' foraging effort and was higher to the north-east of the colony in 1998 (Guinet *et al.* 2001). As prey was located deeper in the water column in this year, travelling to the prey became a significant component of the diving time budget (Boyd 1997) effectively reducing the amount of time available for prey handling. The poor body condition of females during this year may have been another contributing factor. Increased levels of surface swimming, as indicated by greater distances travelled from the colony in 2000, are thought to incur higher energetic costs (Arnould *et al.* 1996a; Costa *et al.* 2000) and may not have been sustainable in 1998. Better body condition and generally higher levels of prey abundance and accessibility at shallower depths in 2000 may have allowed females to reduce costs associated with competition from other seals by foraging further a field.

The proportion of time spent diving (TSD) during trips at sea has also been used as a measure of foraging effort in several studies of otariid foraging behaviour (Arnould *et al.* 1996a; Boyd 1999). TSD was negatively correlated with the amount of time spent at sea (Chapter 2, Boyd 1999) and positively related to at-sea field metabolic rate (Costa and Gales 2000). Surprisingly at Cap Noir, the proportion of time spent diving per foraging trip reached a peak in 1999, rather than the year of lowest prey availability. This is consistent with Boyd's (1999) results for fur seals at South Georgia where foraging effort did not increase in response to reduced prey availability, as females were perhaps operating close their maximum sustained metabolic rate. Thus, at Cap Noir, we would have expected an increase in TSD over the three seasons, as trips became shorter and prey-capture events more frequent. However this was not the case. In 2000

seals displayed at least two different foraging tactics (Chapter 5). Some animals travelled south to regions of cooler SST, while others travelled north-east to pelagic waters characterised by warmer SST. The combination of increased distances travelled during this year and the variability in diving activity between nights spent foraging within the two regions, may have prevented the detection of a clear trend in foraging effort between years. In short, increased food availability, and probably increased prey intake, over a wider region in 2000, and better maternal condition, appear to have enabled females to adopt a greater range of foraging tactics during this year without a corresponding increase in foraging effort.

6.4.3 Maternal allocation and pup provisioning

Growth rates, average size and body condition in March, were all lowest in 1998, indicating that females were not able to fully compensate for lower levels of prey abundance and quality by altering their foraging behaviour. Our measure of foraging efficiency, the rate of daily mass gain over a foraging cycle, was also significantly lower during that year. Moreover, the mean size of pups for this year was positively related to maternal length (see Guinet *et al.* 2000), indicating that presumably older and more experienced females had a competitive advantage over smaller and younger mothers during periods of environmental stress. A similar relationship has been found for sub-Antarctic fur seals (*A. tropicalis*) at Amsterdam Island in periods of low food availability, where pup growth rates were positively related to maternal length (Georges and Guinet 2000). Thus it would appear that selective pressure may act on different phenotypic traits, such as body length, in relation to different environmental conditions.

Reductions in provisioning rates are common amongst otariids exposed to annual or seasonal changes in prey abundance (Francis *et al.* 1998; Goldsworthy 1999; Georges and Guinet 2000). At South Georgia in a year of low prey availability pup growth rates were negatively related to maternal foraging trip duration (Lunn *et al.* 1993), as was the case for *A. tropicalis* over the course of a year (Georges and Guinet 2000). Although mean trip duration (8.5 days) recorded at Cap Noir is the longest reported for Antarctic fur seals at any breeding site, there was no direct correlation between average growth rates of pups over the study and mean provisioning rates of mothers. Absolute mass gained by a pup, however, was positively related to trip duration, as is the case at Macquarie Island (Guinet *et al.* 1999; Robinson 2002). Interestingly, daily pup mass gain, expressed in relation to the duration of the previous foraging cycle, did differ between years, indicating that females were more efficient at transferring energy to the pup in years of greater prey availability.

Overall, pup growth rates and mean body mass and length were significantly higher in 2000 than in other years. Although prey abundance was higher in 1999 than in 1998, female body

condition did not reach maximum levels until 2000. Population dietary intake was more consistent in 2000 than previous years, consisting primarily of the three species *Gymnoscopelus piabilis*, *G. nicholsi* and *E. subaspera*. Milk sampled from females in 2000, had a significantly higher lipid content than in 1999 (Table 6.9; Chapter 4), and contained high quantities of monounsaturated fatty acids, which reflect a diet high in myctophids (Saito and Murata 1998; Chapter 4). At the population level at least, it appears that the combination of improved maternal body condition, higher and more consistent prey abundance and more consistent foraging trip lengths, combined with more energy-rich milk result in higher mean pup body mass, better body condition and faster growth rates. The degree of individual variation in foraging strategies indicates that trip length alone cannot be used as an index of environmental variability and foraging effort at Cap Noir.

Lunn *et al.* (1993) in their study of weaning masses and growth rates of Antarctic fur seals at South Georgia concluded that variation in the foraging efficiency of mothers was the most likely cause of individual differences in the growth rates of pups under favourable feeding conditions. During such years, inter-sexual differences in growth rates have been reported for Antarctic fur seal pups at Heard and Macquarie islands (Goldsworthy 1995; Guinet *et al.* 1999). In these studies males achieved higher growth rates and body masses over the duration of the lactation period than female pups, which is expected in polygynous mammals where size is an important factor in mating success (Trivers 1972; Trivers and Willard 1973; Maynard-Smith 1980). In this study there was no difference in growth rates between the sexes, although male pups were significantly heavier than female pups in 1999 and heavier and longer in 2000. A recent study of growth rates of northern fur seals from birth to weaning detected differences in absolute growth rates between the sexes from birth to moulting and post-moulting and identified the slowest growth rates for both sexes as occurring during the moulting period (Boltnev *et al.* 1998). Additionally, Donohue *et al.* (2002) have shown that mass specific field metabolic rate of this species peaks during moulting. This study encompassed the moulting period of Antarctic fur seal pups, a period characterised by variable rates of metabolic water production (Lea *et al.* 2002). The lack of differential growth rates between the sexes may be associated with increased energetic requirements at this time. As milk consumption of fur seal pups does not tend to vary between the sexes (Arnould *et al.* 1996b; Donohue 1998; Guinet *et al.* 1999) and growth rates were similar, the observed differences in body mass are likely to be attributable to differences in growth efficiency between the sexes. Male pups are usually heavier at birth (Boyd and McCann 1989: Goldsworthy 1995) and have a higher proportional lean mass than females (Arnould *et al.* 1996b), while fasting metabolic rate is higher in female pups (Costa and Gentry 1986; Arnould *et al.* 2001), as are mass specific rates of mass loss (Guinet *et al.* 1999; Guinet *et al.* 2000). Thus, in years of increased consistency in pup provisioning, such as 2000 at Cap Noir, the

differential utilisation of resources allocated to the pup is likely to account for the disparity in body size achieved by male and female pups.

6.4.4 Implications of sustained climatic anomalies and myctophid fisheries

Climatic seasonality during the breeding season has been shown to be the ultimate determinant of the precisely timed fur seal life-cycle for sub-polar northern fur seals (Trites and Antonelis 1994). Deteriorating weather conditions during the breeding season can negatively affect neonatal survival (Trites and Antonelis 1994), as can changes in prey distribution and abundance (Trillmich and Dellinger 1991; Boyd *et al.* 1994). Climatic anomalies, which affect food availability, may also affect the nutritional status (body condition) of lactating females (this chapter, Lunn and Boyd 1993b), which in turn can influence the growth rate of foetuses (Boyd and McCann 1989; Trites 1991). Birth mass has been correlated with subsequent growth in mass and length of northern fur seals (Boltnev *et al.* 1998); mass at weaning for several species (Lee *et al.* 1991), and pup survival (Baker and Fowler 1992). A decline in mean birth mass of Antarctic fur seals pups, and seal numbers at the study colony on Bird Island, South Georgia from 1980-2000, has been liked to changes in the population structure of krill and long-term changes in the physical environment in the Antarctic Peninsula region (Reid and Croxall 2001). Thus, the possible impacts of climatic variability during the lactation period and its influence on the location, species composition and abundance of prey may affect the reproductive success of seals during several breeding seasons (see Lunn and Boyd 1993a). For a species whose peak pregnancy rates occur over a 12-year period (Payne 1977 in Lunn and Boyd 1993a) this potential lowering of lifetime reproductive potential is not trivial.

Add to this the removal of prey from the ecosystem through fishing during the critical pup-rearing period and reproductive success may be depressed further. A fishery for *Electrona carlsbergi* and associated species (*Gymnoscopelus nicholsi* and *G. piabilis*; Anonymous 1992) occurred in the south-western Atlantic (South Georgia and the Antarctic Peninsula) in the 1980s (Kock 1992) and in 1991/92, Russian and Ukranian vessels caught 51 915 tonnes of myctophids in this region (CCAMLR 2002). Since then six countries have attempted to fish for myctophids, primarily in the South Georgia region (CCAMLR sub-area 483). In recent years, many studies have confirmed the importance of myctophids in the diet of marine predators across the Southern Ocean (Chapter 4; Sabourenkov 1991; Reid 1995; Cherel *et al.* 1996; Guinet *et al.* 1996; Reid and Arnould 1996; Cherel *et al.* 1997; Goldsworthy *et al.* 1997; Green *et al.* 1997; Klages and Bester 1998; Raclot *et al.* 1998; Robinson 2002). Should a re-introduction of a myctophid fishery be considered by CCAMLR in the future, the consumption of marine predators will need to be factored into predictive ecosystem models. This study has also provided evidence to suggest that in years characterised by low food availability and anomalous SST, the consumption of other species by fur seals, such as the commercial *Champsocephalus*

gunnari, can be important in terms of overall prey consumption (14% estimated prey biomass; Chapter 4). Continued commercial fishing of this species could conceivably affect the ability of seals to adjust for changes to their regular diet under anomalous environmental conditions. Should the frequency and scale of climatic anomalies increase in the vicinity of the Kerguelen Archipelago, as appears to be the case in recent years (Fig. 6.19), the ability of a female Antarctic fur seal to maintain her own energy requirements in addition to those of her pup may be compromised.

6.4.5 Conclusions and future research

By using a novel multidisciplinary approach over three consecutive breeding seasons, this study has demonstrated that Antarctic fur seals display considerable plasticity in foraging strategies at the Kerguelen Archipelago during the course of the study and when compared to populations at other sites. Inter-annual variability in prey availability and changes in oceanographic conditions were clearly reflected in many aspects of their foraging ecology and provisioning behaviour. Individual variation around mean maternal foraging trip duration (provisioning variability) and maternal foraging efficiency (daily pup mass gain during a foraging cycle) of Antarctic fur seals were two parameters that could be considered as proxies for the availability of the three main prey species (*Gymnoscopelus nicholsi, G. piabilis* and *E. subaspera*) in these years. Other parameters such as the body condition of mothers and pups, pup growth rates and body mass also varied considerably in relation to changes in the marine environment. Thus it would appear that the foraging activity of a top marine predator, such as the Antarctic fur seal, is an effective indicator of environmental variability and myctophid abundance in the upper water column in the Kerguelen region.

The interpretation of findings regarding maternal body condition was slightly ambiguous owing to a lack of knowledge regarding the over-wintering behaviour of female fur seals. Is the nutritional status of females late in lactation merely a function of food availability during the breeding season or, as is more likely, are levels of prey consumption over winter during gestation equally important? Do female deals remain within the vicinity of breeding sites at this time, as is the case at Macquarie Island (Goldworthy 1999) or do they travel south to productive Antarctic waters, as do other myctophid consumers such as the King penguin (Charrassin and Bost 2001). Future studies of this part of female Antarctic fur seal's annual cycle are necessary to fully understand the links between environmental variability and the acquisition and allocation of resources at all breeding sites.

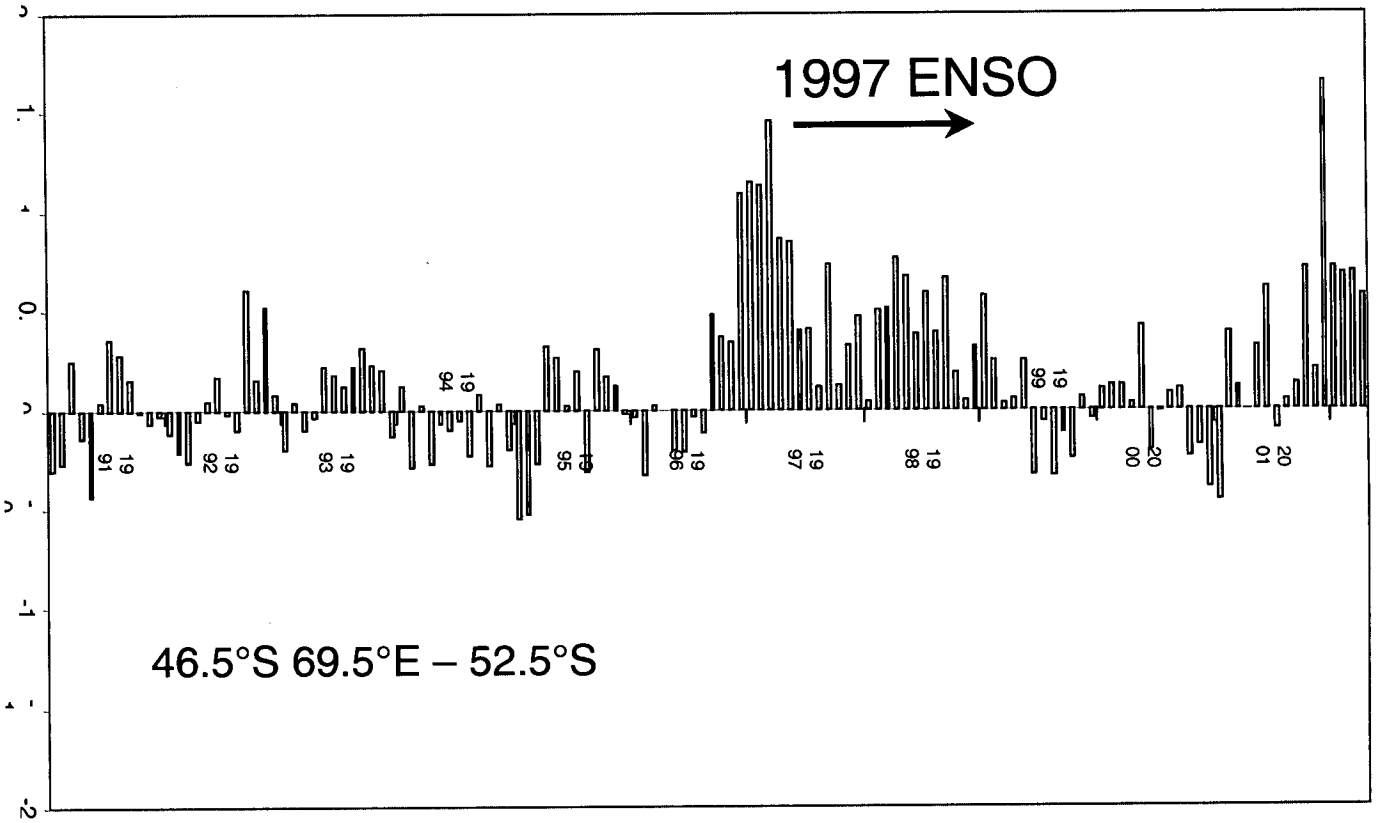


Figure 6.19 Monthly sea surface temperature anomaly (SSTA) data from ship, buoy and bias-corrected satellite data from 1991-2002 (Reynolds and Smith 1994), in an area encompassing the foraging zones of Antarctic fur seals (1998-2000, pink bars). Coloured bars denote positive (red) and negative SSTA (°C).

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APPENDIX

Summary dive statistics of female Antarctic fur seals from Îles Kerguelen (1998-2000)

Seal	Year	Departure date	Season	TDR type	Trip length (days)	BDG	No. dives ≥4m	Dive duration (min)				Depth (m)			
								Max.	Mean	sd	Median	Max.	Mean	sd	Median
0	1998	06/02/98	2	PTT5	7.4	1	1323	3.3	1.7	0.37	1.7	135	72	14	70
1	1998	06/02/98	2	PTT5	5.7	1	885	4.3	2.1	0.56	2.2	170	80	32	80
1	1999	31/01/99	2	PTT	7.1	1	1372	3.9	1.9	0.70	1.9	187	66	30	63
10	1998	22/02/98	2	MK6	11.4	4	1956	4.4	1.7	0.98	2.0	180	65	42	71
2	1998	07/02/98	2	PTT5	8.1	1	1104	3.5	1.8	0.46	1.8	160	55	19	53
26	1999	10/01/99	2	MK6	8.0	2	2221	4.4	1.0	0.86	0.8	186	35	33	27
3	1998	08/02/98	2	PTT5	3.0	1	484	3.7	1.9	0.41	1.8	164	85	26	88
37	1998	11/02/98	2	PTT5	7.0	1	756	4.6	2.6	0.76	2.7	236	113	37	119
4	1998	06/02/98	2	MK6	14.1	1	2114	3.7	2.1	0.49	2.0	154	57	24	50
41	1998	12/02/98	2	MK6	17.9	3	1174	3.8	1.4	0.73	1.4	138	54	31	48
41	1999	10/02/99	2	MK6	13.0	1	1750	3.8	1.7	0.67	1.8	162	63	27	66
42	1998	12/02/98	1	PTT5	16.5	3	2654	3.7	1.0	0.88	0.6	180	37	38	14
43	1998	12/02/98	2	PTT5	5.0	1	463	3.5	2.1	0.49	2.2	165	88	26	92
46	1998	15/02/98	2	MK6	11.6	3	1508	3.8	0.9	0.88	0.4	156	32	34	10
47	1998	14/02/98	2	PTT5	8.4	4	588	4.0	2.0	0.70	2.0	146	70	30	71
5	1998	07/02/98	2	MK6	10.7	1	1931	3.2	1.6	0.65	1.8	146	58	34	65
51	1998	15/02/98	2	PTT5	3.9	1	466	4.1	2.3	0.69	2.4	161	83	34	89
52	1998	19/02/98	2	PTT5	6.8	1	1153	4.1	1.7	0.81	1.6	175	48	43	32
54	1998	20/02/98	2	MK6	16.9	3	6467	4.0	0.5	0.60	0.3	172	16	20	10
55	1998	20/02/98	2	PTT5	7.0	1	1254	3.8	1.6	0.78	1.8	181	63	40	67
55	1999	02/02/99	2	PTT5	6.5	1	1177	3.9	1.8	0.70	1.8	178	67	30	62
56	1998	23/02/98	2	MK6	7.1	1	1361	4.5	2.1	0.87	2.2	208	79	51	90
57	1998	25/02/98	2	PTT5	5.9	1	1117	3.4	1.9	0.65	1.9	172	79	38	79
57	1999	05/02/99	2	PTT	4.0	1	821	3.5	2.0	0.74	2.1	156	79	37	88
6	1998	07/02/98	2	MK6	3.3	1	499	3.4	1.8	0.47	1.8	162	63	28	62
7	1998	07/02/98	2	MK6	10.3	3	1660	3.7	1.5	0.77	1.5	148	50	31	50
8	1998	06/02/98	2	MK6	6.9	1	942	4.2	2.2	0.58	2.3	187	82	28	86
C1	1999	26/01/99	2	MK6	4.0	2	1648	3.7	1.0	0.80	0.8	142	32	26	22
C2	1999	27/01/99	2	MK6	4.3	1	853	4.1	2.1	0.61	1.9	164	63	27	54
C3	1999	02/02/99	2	MK6	9.6	2	1758	3.7	1.4	0.78	1.5	170	43	26	46
C4	1999	01/02/99	2	MK6	6.6	1	1303	4.2	1.9	0.82	2.0	138	64	35	66
C5	2000	30/01/00	2	MK6	8.3	2	2862	3.8	0.9	0.73	0.8	176	31	29	22
F10	2000	17/02/00	2	MK7	3.9	1	751	3.9	1.7	0.44	1.8	191	58	28	48
F11	2000	19/02/00	2	MK7	9.0	1	1519	4.4	2.0	0.61	2.1	185	71	39	74
F12	2000	20/02/00	2	MK7	9.4	2	2077	4.2	1.5	0.80	1.4	177	42	39	24
F2	2000	03/02/00	2	MK7	6.3	1	861	3.7	1.6	0.60	1.6	183	75	35	83
F3	2000	04/02/00	2	MK7	9.0	2	2256	3.7	1.1	0.76	1.0	181	40	33	33
F5	2000	07/02/00	2	MK7	8.8	2	2355	3.3	0.9	0.58	0.7	138	33	20	32
F6	2000	05/02/00	2	MK7	12.0	2	3091	4.8	1.2	0.75	1.2	191	45	35	33
F7	2000	17/02/00	2	MK7	10.0	2	2516	3.8	1.2	0.87	1.0	193	38	35	20.5
F9	2000	18/02/00	2	MK7	12.3	2	2652	3.4	1.2	0.63	1.3	176	42	32	33
H2	2000	15/01/00	1	PTT	6.8	1	1163	2.5	1.1	0.40	1.1	216	62	27	60
H3	2000	29/01/00	2	PTT	12.3	3	2453	3.5	0.9	0.83	0.6	158	32	32	19
H4	2000	30/01/00	2	PTT	8.9	1	2055	3.3	1.5	0.68	1.7	161	64	34	73
H5	2000	30/01/00	2	PTT	6.2	1	1141	3.9	1.5	0.81	1.7	157	39	29	34
H6	2000	31/01/00	2	PTT	9.3	2	2863	4.3	1.1	0.70	0.8	177	41	26	34
H7	2000	29/01/00	2	PTT	8.8	2	2855	3.3	1.1	0.66	1.0	162	35	27	25
H8	2000	31/01/00	2	PTT	5.2	1	915	3.8	1.7	0.66	1.8	175	65	34	71
H9	2000	02/02/00	2	PTT	8.3	2	2032	4.5	1.2	0.68	1.1	202	44	25	43
IN1	2000	07/01/00	1	PTT5	8.7	1	2155	3.3	1.5	0.58	1.5	162	62	35	47
IN10	2000	06/01/00	1	MK7	8.3	2	2226	4.1	1.3	0.85	1.0	172	48	30	36
IN11	2000	08/01/00	1	MK7	6.5	4	1178	3.5	2.1	0.52	2.3	181	93	39	105
IN12	2000	06/01/00	1	MK7	9.1	2	2847	3.3	1.2	0.65	1.0	155	41	29	30
IN13	2000	08/01/00	1	MK7	9.0	1	1674	4.1	1.5	0.79	1.4	186	51	35	37
IN14	2000	07/01/00	1	MK7	8.2	2	2335	3.8	1.3	0.71	1.3	171	47	28	38
IN15	2000	08/01/00	1	MK7	6.9	1	1367	3.7	1.8	0.65	1.9	152	67	36	57
IN2	2000	06/01/00	1	PTT5	8.8	1	2015	4.3	1.4	0.79	1.2	167	45	34	33
IN3	2000	05/01/00	1	PTT5	7.5	1	1410	3.8	1.6	0.64	1.5	155	49	31	36
IN4	2000	05/01/00	1	PTT5	8.9	3	1718	3.5	1.1	0.76	0.9	142	37	28	31
IN5	2000	08/01/00	1	PTT5	11.4	1	1809	3.3	1.8	0.58	1.7	185	59	39	44
IN7	2000	07/01/00	1	PTT5	8.3	1	1845	3.7	1.9	0.92	2.2	134	61	35	62
IN8	2000	05/01/00	1	MK7	7.3	1	1213	3.6	1.8	0.70	2.0	168	71	43	58
J1	2000	07/01/00	1	MK7	6.0	2	1213	3.8	1.6	0.52	1.5	143	46	22	40
J10	2000	08/01/00	1	MK7	4.3	2	1299	4.0	1.0	0.68	0.9	163	35	24	30
J2	2000	07/01/00	1	MK7	3.2	2	706	3.8	1.3	0.58	1.3	139	44	23	40.5
J3	2000	06/01/00	1	MK7	5.1	2	1118	3.4	1.4	0.49	1.3	159	45	23	39
J6	2000	07/01/00	1	MK7	8.1	2	2230	3.6	1.2	0.68	1.1	156	46	30	36
J7	2000	08/01/00	1	MK7	7.9	2	2186	5.3	1.3	1.00	0.9	240	43	40	28.5
J9	2000	08/01/00	1	MK7	5.8	2	1100	4.2	1.2	0.71	1.2	155	43	24	42
K1	2000	18/12/99	1	MK7	4.1	1	734	4.8	2.1	0.80	2.0	201	61	34	50

Seal	Year	Departure date	Season	TDR type	Trip length (days)	BDG	No. dives ≥4m	Dive duration (min)				Depth (m)			
								Max.	Mean	Seal	Year	Max.	Mean	Seal	Year
K3	2000	21/12/99	1	MK7	5.4	2	988	4.2	1.6	0.65	1.6	131	45	21	38
K4	2000	18/12/99	1	MK7	5.2	1	906	3.8	1.9	0.54	1.8	168	59	25	53
K5	2000	20/12/99	1	MK7	5.2	2	943	3.1	1.2	0.51	1.2	143	43	24	36
K7	2000	23/12/99	1	MK7	5.1	2	1051	3.8	1.5	0.80	1.6	158	35	26	27
K8	2000	25/12/99	1	MK7	7.8	3	1365	3.8	1.1	1.05	0.4	158	29	30	13
K9	2000	20/12/99	1	MK7	4.7	1	644	4.5	2.0	0.76	2.0	166	55	28	50.5
K10	2000	21/12/99	1	MK7	4.7	1	1194	3.7	1.6	0.73	1.4	202	57	37	41
L1	1999	19/01/99	2	PTT	4.2	1	872	3.9	2.0	0.66	2.0	131	45	25	35
L2	1999	20/01/99	2	PTT	6.1	2	1544	4.1	1.7	0.86	1.5	179	50	33	41
L3	1999	21/01/99	2	PTT	10.0	2	2881	4.3	1.4	0.89	1.1	155	40	28.7	29
L4	1999	21/01/99	2	PTT	4.9	2	1206	4.3	1.6	0.81	1.4	157	47	26	40
L5	1999	23/01/99	2	PTT	7.2	1	1286	3.8	1.8	0.78	1.8	156	61	29	63
L7	1999	09/02/99	2	PTT	15.9	3	3231	3.8	1.1	0.87	1.1	175	39	34	25
L8	1999	10/02/99	2	PTT	5.0	1	889	3.8	2.3	0.83	2.5	173	91	38	97
L9	2000	12/02/99	2	MK7	6.0	1	864	2.9	1.7	0.36	1.6	130	63	14	61
L9	1999	22/12/99	1	PTT	9.1	2	2912	3.3	0.9	0.96	0.3	144	31	36	9
P1	2000	16/12/99	1	PTT	6.2	1	1265	4.4	1.6	0.87	1.5	186	53	37	44
P2	2000	16/12/99	1	PTT	6.1	2	1177	3.0	1.1	0.50	1.0	117	41	14	39
P3	2000	16/12/99	1	PTT	6.2	1	898	3.6	1.6	0.68	1.7	156	41	22	38
P4	2000	21/12/99	1	PTT	5.6	2	1070	3.0	1.4	0.60	1.3	140	43	18	42
P5	2000	16/12/99	1	PTT	3.0	1	337	3.8	2.0	0.58	2.0	155	59	23	59
P6	2000	17/12/99	1	PTT	4.1	1	588	3.6	1.9	0.47	1.8	119	39	15	34
P8	2000	22/12/99	1	PTT	9.9	2	2459	4.2	1.3	0.67	1.1	174	44	26	36
P9	2000	22/12/99	1	PTT	5.4	2	1197	3.3	1.5	0.50	1.4	145	44	23	37
S1	2000	12/02/00	2	PTT	9.1	2	1863	3.6	1.6	0.7	1.6	138	44	24.7	44
S2	2000	17/02/00	2	PTT	4.0	1	567	3.8	2.4	0.53	2.3	186	98	26	103
S3	2000	18/02/00	2	PTT	6.0	1	854	3.5	2.0	0.47	2.1	150	76	30	80
S4	2000	24/02/00	2	PTT	10.4	2	3129	3.7	0.9	0.56	0.8	151	25	18	21
S5	2000	28/02/00	2	PTT	12.0	2	5024	4.3	0.7	0.62	0.7	212	25	22	24
T1	1999	18/12/98	1	PTT	8.0	1	1671	3.9	1.7	0.80	1.6	168	54	35	39
T2	1999	18/12/98	1	PTT	8.7	2	2711	3.6	1.1	0.64	0.9	144	36	25	27
T3	2000	07/01/00	1	PTT	2.8	2	694	3.2	1.2	0.49	1.1	138	51	19	46
T3	1999	18/12/98	1	PTT	6.0	2	2271	3.6	1.2	0.89	0.8	131	36	31	20
T5	1999	27/12/98	1	PTT	2.7	1	712	3.9	1.7	0.77	1.5	140	45	28	33
T6	1999	29/12/98	1	PTT	5.7	1	1493	4.0	2.1	0.74	1.8	157	55	34	42
T7	1999	29/12/98	1	PTT	3.4	1	669	4.8	2.1	0.68	1.9	151	50	32	36
T8	1999	29/12/98	1	PTT	5.1	1	1147	3.3	1.9	0.58	1.8	125	45	27	29
x1	1999	07/01/99	1	MK7	4.3	1	1207	3.6	1.9	0.63	1.8	159	51	28	45
x10	1999	20/01/99	2	MK7	10.2	2	3378	2.7	0.9	0.53	0.9	118	29	19	24
x11	1999	19/02/99	2	MK7	5.0	2	1080	3.9	1.4	0.84	1.5	187	54	32	51
x2	1999	05/01/99	1	MK7	14.4	2	4146	3.6	1.0	0.76	1.1	191	34	30	30
x3	1999	05/01/99	1	MK7	2.9	1	658	3.9	2.3	0.64	2.3	163	66	33	51
x4	1999	06/01/99	1	MK7	4.8	2	1328	4.1	1.4	0.65	1.3	171	49	26	41
x6	1999	14/01/99	1	MK7	8.8	2	2690	4.1	1.0	0.74	1.0	210	39	32	29
x7	1999	14/01/99	1	MK7	4.0	1	1012	3.5	1.4	0.75	1.3	136	44	29	36
x8	1999	13/01/99	1	MK7	4.9	1	1193	3.8	1.9	0.71	2.1	162	61	29	62
x9	1999	17/01/99	1	MK7	5.3	1	1195	4.0	1.8	0.89	1.8	191	62	37	60

Season 1 dates <20 Jan; Season 2 dates ≥20 Jan; PTT=PTT+Mk7 TDR; PTT5=PTT+Mk5 TDR; BDG – Behavioural dive group